Studies on the Structure and Classification of the Digenetic Trematodes.

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With Plates 9, 10.

The following work was commenced about the middle of 1907 at the Gatty Marine Laboratory, St. Andrews, under the Carnegie Trust Research Scheme. The greater part of it was done privately in the Pathological Laboratory, University College, Dundee, and it was concluded at the Marine Biological Laboratory, Millport, under a Government (Royal Society) Grant.

My best thanks are due to very many friends for assistance in various directions, and in particular to Professor McIntosh, of St. Andrews, for continual encouragement and suggestions, and to Professor Sutherland, of University College, Dundee, for granting me the privilege of working in his laboratory and for helping to elucidate several pathological difficulties.

In this paper an attempt has been made to allocate each of the forms dealt with to its approximate systematic place—a matter of considerable difficulty in many cases. At the present time a classification of the digenetic Trematodes in the true sense of the term can hardly be said to exist. To attempt to define a higher systematic unit than the genus is attended with much risk. A considerable number of subfamilies have certainly been created, but few of these consist of more than two or three genera, and are really at most to be considered as indications according to which classification may be expected to proceed. The formation, however, of

these groups or sub-families and the examination of their relationships seems to be of the greatest importance in leading up to the natural family groups. On that account I have endeavoured—not in every case with success—to include each of the genera described here in some sub-family group.

Many systematic difficulties have been encountered in the course of this work, and I should like here to refer to the case of Campula oblonga Cobbold. It is almost a certainty that the form I am describing as Brachycladium oblongum (Brn.) is actually identical with Cobbold's species, but according to the strict laws of nomenclature the name not only of Cobbold's genus but also of his species must be regarded as nomen nudum. I have followed in this matter the authority of Looss and Odhner, but it seems to me that this particular species has been submitted to a test which, were it to be applied as rigorously, would prove fatal to many of the species and genera of older writers. There appears to be no escape from the trammels of nomenclature, and the only hope of simplifying matters consists in the submittal of each new or re-described species or other systematic unit to as strict a scrutiny as has been done in the case of Campula oblonga. This can never be done effectually so long as the work of criticism remains in the hands of isolated individuals. There is undoubtedly a need for some central scheme, as has been already advocated more than once.

The general anatomy and histology of the Trematoda has been the subject of fairly exhaustive reseach, yet a few points still remain doubtful and disputable, e.g. the function of the so-called subcutaneous glands and the large cells of the suckers. The myoblastic nature of these cells, as demonstrated by Bettendorf, can hardly be said to have been conclusively proved, or at any rate some modification and extension of Bettendorf's original views is necessary. The large cells of the suckers appear to have little in common with the subcutaneous cells. In appearance and staining properties they resemble true nerve-ganglion cells. The subcutaneous cells bear a much closer resemblance to the small cells of the suckers.

Few new results of a general nature are offered in the following notes. On the other hand, there are many apparent redundancies. These are only to be excused on the ground that the tendency to increased differentiation of specific forms, together with the fact that in numerous cases a form previously considered as a single species has on careful study of its anatomy and histology been subdivided into two or more distinct species, renders it necessary to give as full a description of the form dealt with as possible. In this connection reference to a much discussed paper of Stafford's[1] can hardly be omitted. Looss[2] has already expressed what must be the opinion of every systematist on this paper. Such a method as Stafford has employed is unpardonable even in a "preliminary contribution," and can hardly fail to cause endless trouble and confusion. By the laws of nomenclature Stafford's generic names, except where preoccupied, must be regarded as valid, for he is presumed to have in his possession type-specimens of the several genera which he has named, or at any rate type-specimens must be supposed to exist somewhere.[3]

For this reason Stafford's generic name Fellodistomum has been adopted here, although strictly speaking the name Fellodistomum is really synonymous with Leioderma Staff. (and therefore with Steringophorus Odhn.), for there is absolutely no difference of generic importance in Stafford's definitions of the two genera. His definition of Fellodistomum is actually a recapitulation of his definition of the preceding genus Leioderma, and the only difference is summed up in the sentence, "Many resemblances to Leioderma, but with sucker and genital glands crowded backwards." No mention is made of the position of the genital aperture, the absence of œsophagus, or the condition of the

[1] "Trematodes from Canadian Fishes," in 'Zool. Anzeig.,' xxvii (1904), pp. 481–495.

[2] "Revision of Hemiuridæ," in 'Zool. Anzeig.,' xxxi (1907), pp. 587–620.

[3] Unfortunately this does not work out satisfactorily in every case. To my request (July, 1908) for type-specimens of several of his genera Dr. Stafford has vouchsafed no reply.

uterus and ova, which, as Odhner has in part indicated, and as I have tried to show, are really the generic features distinguishing Fellodistomum from Steringophorus.

Amongst the various histological features to which attention has been paid are the size of the muscle-fibres and of the elements of cellular structures. These, however, depending as they do so much on the state of contraction and the method of preservation, can hardly be considered of much practical utility. Other features of more importance which have been dealt with are the nature of the yolk-gland secretion (see under Stephanophiala laureata), the intestinal epithelium, and the cellular elements of the suckers in Fellodistomum fellis.

Reference may be made here to an interesting bionomic problem, which unfortunately does not admit of easy solution, namely, the length of time required for the cercaria to attain maturity on entering its final host. It is easily ascertainable that it does not commence to produce ova, which may be regarded as the criterion of maturity, immediately on entering its host. A longer or shorter period of time usually elapses, during which it increases considerably in size. The question has occurred to me in connection with various species, and here particularly in the case of Lebouria idonea. It has been a matter of frequent observation that a certain definite size limit exists between immature and mature specimens, or, in other words, that egg-production begins at a more or less constant period. In the case of Lebouria idonea the smallest mature specimen measured 1·6 mm. and the largest immature specimen was of the same length. Again, in Podocotyle atomon the limit of maturity appears to lie somewhere between ·9 mm. and 1·0 mm. Many other examples might be given, but these will serve as illustrations. The smallest individuals found in the above two cases measured respectively 1·0 and ·65 mm. It is fairly certain, however, that the cercariæ in each case are somewhat smaller than the above minimum limits, but taking them at those lengths it is evident that the cercariæ must

increase in length by at least half before attaining sexual maturity. This, of course, does not hold good in every instance, for in some species the proportionate increase is smaller, while in others it is larger.[1]

That Distomids, like other animals, have a fairly constant maturity-size might have been deduced from analogy. The production of ova as the test of maturity is open to obvious objections. It might be held that the animal is mature when the genitalia are developed, and that egg-production need not proceed immediately although the animal continues to grow. Against this must be put the fact of the constant line of demarcation in size between specimens with ova and those without, and further, that a Distomid of adult size without ova is a rarity. Admitting that such a line of demarcation does exist, and that it is constant within close limits of variation, we should here have what might possibly be a valuable aid to diagnosis between nearly related species. As an example might be taken the case of the species of the genus Levinseniella. I have previously described a mixture of two or more of these as Spelotrema feriatum n. sp. (see later). They were found in five different species of birds. In three of these the Distomids were fully mature, but in the other two, namely, Hæmatopus and Vanellus, they were quite immature, although of the same size, or even larger. I have examined several specimens of both these birds at different seasons of the year and found the parasites fairly frequently, but never in the mature state. The probability is that the latter specimens represent a species distinct from that occurring in Ægialitis and Pelidna.

In the determination of the identity of similar parasites occurring in different hosts certain additional factors may enter, and it is to these that at several times by various authors variations in a particular Distomid inhabiting more than one final host have been ascribed. Differences of less or greater degree in external and internal characters, amounting in

[1] Looss deals with the same matter in "Distomen unserer Fische und Frösche," 'Bibliotheca Zool.,' vi (1894), p. 240.

many cases, as easily proved by later research, to specific distinction, have been attributed to the different environmental conditions in different hosts. That the variation in such cases is to be explained by the environment is not at all certain, and it is very probable that on careful examination the same amount of variation would be found in specimens collected from the same host. Certain features are capable of varying within comparatively wide limits and can be measured with sufficient precision, e. g. the size of the ova and the extent of the yolk-glands. A case in point is that of Podocotyle atomon (Rud.), which occurs in a large number of different fish. In this species the ova were found to vary considerably in size, and a list was given[1] of the size of the ova in specimens from four different hosts, which apparently showed that there were different limits of variation in each case. These measurements included a fair number of examples, but not nearly sufficient to determine the utmost limits in each host. One thing the list does show, however, is that in no particular species of fish are the ova distinct in size; such a variation, otherwise, would be sufficient to indicate specific distinction. I have since found in a single specimen of Gastræa spinachia a species of Podocotyle with ova greatly exceeding those from the fish already referred to and yet not differing in other respects from Podocotyle atomon. It is difficult, on this account, to say what effect, if any, environment may have on Distomid parasites, or whether the observed variations are purely the result of fortuitous circumstances. The question appears worth solving, and I hope to be able to publish later some observations on the same species found in numerous fishes from the west coast of Scotland.

The following is a list of the species mentioned in this paper, with their hosts and habitat:

[1] "Entozoa of British Marine Fishes," in 'Annals and Mag. Nat. Hist.' (7) xix, p. 76.

Stephanophiala (n.g.) laureata (Zed.)	Salmo fario	Intestine.
Stephanophiala transmarina n. sp.	Salvelinus fontinalis Salmo mykiss	Intestine.
Brachycladium oblongum (Brn.)	Phocæna communis	Liver.
Brachycladium sp.	Phocæna communis	Liver.
Lebouria (n. g.) idonea n. sp.	Annarrhichas lupus.	Intestine.
Lebouria obducta n. sp.	Bairdiella chrysura	Intestine.
(Lebouria) tumidula (Rud.) ?	Labrus bergylta	Intestine.
Podocotyle atomon (Rud.)	Pleuronectes flesus	Intestine.
= Dist. vitellosum Johnstone	Pleuronectes platessa. Gadus virens. Gadus pollachius.	
Cainocreadium (n. g.) labracis (Duj.)	Labrax lupus	Intestine.
Peracreadium (n. g.) genu (Rud.)	Labrus bergylta	Intestine.
Peracreadium commune (Olsson)	Labrus bergylta	Intestine.
(Lepocreadium) serospinosum sp. inq.	Leiostomus xanthurus	Intestine.
= Dist. globiporum Linton e.p.		
Zoogonus rubellus (Olsson)	Anarrhichas lupus	Intestine.
Fellodistomum fellis (Olsson)	Anarrhichas lupus	Gall-bladder
Fellodistomum agnotum n. sp.	Anarrhichas lupus	Gall-bladder and duodenum.
Steringophorus cluthensis n. sp.	Pleuronectes microcephalus	Intestine.
Plagiorchis notabilis n. sp.	Anthus obscurus Motacilla flava	Intestine.
Spelotrema claviforme (Brandes)	Pelidna alpina Ægialitis hiaticula Anthus obscurus Numenius arquata Motacilla flava Larus ridibundus	Intestine, cæca and rectum.
Spelotrema simile Jägersk.	Larus ridibundus	
Spelotrema excellens Nicoll	Larus argentatus	Intestine and cæca.
Levinseniella brachysoma (Crepl.) = Spelotrema feriatum mihi, e.p.	Pelidna alpina Totanus calidris Ægialitis hiaticula	Intestine, cæca and rectum.
Levinseniella sp. = Spelotrema feriatum mihi, e.p.	Hæmatopus ostralegus Vanellus vanellus Numenius arquata Larus ridibundus	Intestine, cæca and rectum.
Tocotrema jejunum Nicoll	Totanus calidris	Intestine.

Cryptocotyle concava (Crepl.)	Phalacrocorax graculus	Intestine, cæca and rectum.
Gymnophallus dapsilis Nicoll	Oidemia nigra	Bursa Fabricii.
	Oidemia fusca	
Maritrema humile Nicoll	Totanus calidris	Intestine.
Maritrema lepidum Nicoll	Larus argentatus	Intestine.
Maritrema gratiosum Nicoll	Larus ridibundus	Intestine.
	Pelidna alpina	
	Ægialitis hiaticula	
	Hæmatopus ostralegus	

Sub-family Stephanophialinæ, n. sub-fam.

Genus Stephanophiala, n. g.

Stephanophiala laureata (Zeder). Pl. 9, figs. 1–5.

Distoma laureatum Zeder, 'Nacht. z. Naturg. d. Eingeweidew.,' p. 192; Rudolphi, 'Entoz. Hist.,' ii, p. 413; 'Synops.,' pp. 113 and 413; Dujardin, 'Hist. d. Helminth,' p. 435; Olsson, 'Kgl. Sv. Vet. Akad. Handl.,' 1876, Nr. 1, p. 21, Pl. iv, figs. 52–54; ? Linton, 'Rept. U.S. Commiss. Fisheries for 1889–1891' (published 1893), p. 553, fig. 26–30.

Distoma farionis Müll. Blanchard, 'Mem. Soc. Zool. France,' iv, 1891, pp. 481–3, fig. 38.

Crepidostomum laureatum (Zed.) Braun, 'Annal. Hofmus. Wien.,' xv, pp. 231, 232; Looss, 'Zool. Jahrbüch. Abtheil. Syst.,' xvi, 1902, p. 452.

This fairly frequent parasite of the common trout (Salmo fario) has been known for many years, and it has been found by various observers, who have each contributed towards a knowledge of the species, but no connected account has appeared since Olsson's description in 1876. Although not entirely free from error, this description is fairly accurate, but it is not sufficiently detailed for modern requirements.

Blanchard completed the topography of the female genitalia, and Looss was the first to indicate the structure of the circum-oral papillæ. Several other important features remain undetermined. The systematic position of the species will be discussed after a general account of its anatomy has been given.

The distribution of this Trematode may not be confined to Europe, for Linton has described what appears to be the same or a closely related species from an American trout (Salmo mykiss). No difference of specific importance is to be found in Linton's description, but it is probable that the two forms are not quite identical (see p. 35).

My specimens were obtained in June, 1907, from two small trout captured in a tributary of the River Spey (North of Scotland). Each fish contained four or five examples of the parasite. In another two small trout, from a stream running into the River Tay (April, 1907) several immature specimens (fig. 5) were found. The intestine of one of these fish was absolutely crammed full of Echinorhynchus angustatus Rud. while only one Distome was present. This might afford a striking instance of what Hausmann[1] terms the mutual crowding-out of parasites. Still another trout, of large size but in poor condition, was obtained later from the River Tay, but it contained no Trematodes. Four small trout were examined in May, 1908. They were also from the basin of the River Tay, but they did not contain Distomum laureatum. A few specimens, however, of Bunodera nodulosa (Zed.) were found in them. Olsson found the parasite from April to August, and Linton in July and August. I have had no opportunity of ascertaining whether it was present during the other months of the year. The occurrence in April of immature specimens only is suggestive, but my material is obviously inadequate to admit of any conclusion with regard to the life-history.

[1] "Über Trematoden der Süsswasserfische," 'Revue Suisse Zool.,' v. This, however, can only be regarded as an occasional occurrence except in particular instances.

The number of specimens occurring in one host is not very great, although Linton puts it at as many as one to two dozen. Olsson says he found many specimens, but it is not clear whether he means in each or altogether. Its frequency, however, is well established, and it is probably more often present than not, at any rate during the months of April to August.

The habitat is chiefly the middle reaches of the intestine, but I have found it, especially in the immature state, as far down as the rectum. The occurrence of young specimens at a lower level in the gut than the adults is characteristic of more than one species, and it is probable that the cysts traverse the whole length of the intestine before the cercariæ are set free. Olsson records it from the rectum and stomach of the trout, also from the pyloric appendages of Thymallus vulgaris. Linton found it in the rectum of Salmo mykiss.

It is easily discoverable in the intestinal contents, being moderately large and of a pale but distinctly reddish colour. Olsson says the colour is white, and the difference may be due to the fact that my specimens were not seen till twenty-four hours after the death of the host, at which time the parasites were still alive, but very sluggish. There is no very obvious reason, however, for believing that that would account for a change in colour. For the above reason little movement was observed in the parasite, but it was apparent that the neck or pre-acetabular part was much more mobile than the rest of the body. The shape is elongated oblong, tapering towards either extremity, but more or less rounded according to the state of contraction; flattened dorso-ventrally. The continuity of the anterior margin is interrupted by the projection of two or more of the circum-oral papillæ. The surface of the body was thrown into irregular rugæ, but that is commonly seen in Trematodes some time after the death of their host. The length of my mature specimens is fairly uniform—3–4 mm.; the immature specimens are in many cases less than 1 mm. Most observers are agreed in fixing

the limits in size at 2–4 mm., but Olsson found examples measuring as much as 6 mm. The greatest breadth occurs at, or just behind, the ventral sucker, and is approximately one quarter of the length. This proportion is fairly constant.

The suckers are well developed and muscular. The oral sucker is sub-terminal and round, but not quite globular. In a specimen of 3·5 mm. length (to which all the following measurements may be referred) its transverse diameter measures ·31 mm., while its antero-posterior diameter is usually slightly greater. Its aperture is not exactly circular, being encroached on laterally, but to no great extent, by the part bearing the two ventral papillæ. The wall of the sucker is not of the same thickness throughout, the anterior dorsal part being much thicker than the remainder. Here the thickness is ·093 mm.; the rest of the wall varied from ·05 mm. to ·065 mm. It presents a further peculiarity in that the thick anterior part is separated from the rest by a distinct constriction where the thickness is not more than ·035–·04 mm. The appearance suggests that the thick anterior part is a secondary growth from the main part of the sucker. The histological structure of the sucker represents what must be regarded as the typical Distomid structure. Externally it is separated from the body parenchyma by a well-defined fibrous membrane. Its cavity is lined by a cuticular layer continuous with the body cuticle, but somewhat thinner. Beneath this is a thin fibrous membrane continuous with the external membrane. Between the external and internal membranes run the radial muscle-fibres arranged in groups, each containing from six to twelve fibres. The latter may attain a diameter of ·0045 mm., but this naturally varies with the state of contraction and is usually not more than ·002 mm. The groups are separated from each other by spaces in which lie one or more cells. The anterior swelling is also traversed by radial fibres more closely arranged, and radiating, fan-like, from the inner membrane to the outer. Their course is not straight but curved (fig. 2). Close beneath each membrane there is a series of circular muscle-fibres, arranged

singly, one fibre being situated between the ends of adjacent radial fibres. Their diameter is about ·0006–·0013 mm., but the fibres of the external layer are somewhat stouter than those of the internal layer. Two distinct varieties of cells are met with in the sucker. The most numerous are small, rounded cells, which stain uniformly purple with hæmalum-eosin, and their nuclei are differentiated only by their darker colour. They are situated for the most part closer to the external membrane than to the internal membrane. Several filaments are given off by each cell. The other variety of cell is distinguished by being much larger and by different staining reaction. The cell body is not well defined, but the nucleus is large, conspicuous and round or oval in shape. It stains light pink, with a clear zone externally and a more granular zone internally. Within it is a small round nucleolus, staining bright red. These are the myoblasts, and they lie in the spaces between the groups of muscle-fibres and usually midway between the outer and inner membranes of the sucker.

The circum-oral papillæ are, as Looss has already pointed out, outgrowths of the muscle substance of the sucker. They are six in number, two being distinctly ventral and four dorsal, and their bases are all situated on the same transverse plane. The ventral papillæ are closely opposed to the margin of the aperture of the sucker, and their bases, as above mentioned, occasionally give rise to two prominences projecting into the aperture; the other papillæ are situated equidistant from each other and from the ventral papillæ. The shape is depressed, tongue-like; the size varies according to the state of contraction. In a transverse section of their base the measurements are ·035–·04 by ·015–·02 mm., while the length is about ·03–·04 mm. The muscle-fibres of the papillæ are apparently finer than those of the sucker. They comprise both longitudinal and annular fibres. No myoblasts were observed in the substance of the papillæ, but at the base of each, situated in the sucker, there is usually at least one myoblast apparently in connection with the papilla. A

feature of difference between the dorsal and ventral papillæ is due to the fact that the dorsal wall of the sucker is not closely apposed to the dorsal body cuticle, but is separated from it by parenchymatous tissue. The dorsal papillæ in finding their way to the exterior have to pass through this layer, and thus around the base of each dorsal papilla a small swelling is formed by the parenchyma, and this swelling is absent in the case of the ventral papillæ, for at their origin the wall of the sucker is contiguous with the cuticle and there is no intervening tissue. Still another point is to be remarked. The ventral papillæ arise from the already noted anterior swelling of the sucker, but the dorsal papillæ arise from the main part of the sucker, immediately behind the swellings. This is indicated in fig. 2. This circumstance seems to necessitate a modification of the views of Braun and Looss on the origin of the papillæ. It can still be maintained that the anterior swelling, together with the papillæ, represent the almost undivided suctorial swelling in Rhytidodes gelatinosus (R.), but it is evident that in Stephanophiala laureata the process of transformation has gone much further than was supposed. Thus the division of the simple swelling has given rise, not only to distinct contractile papillæ, but four of these have been entirely separated from the original swelling and have been displaced backwards.

The ventral sucker is situated near the junction of the anterior and middle thirds of the body. It is transversely oval and nearly twice as large as the oral sucker. Its transverse diameter is ·50 mm. and the longitudinal diameter ·43 mm., i.e. the diameter is about one seventh of the length of the body. Its depth is ·16 mm. and occupies nearly the whole thickness of the body. The wall has an average thickness of ·057 mm. The histological structure is essentially the same as that of the oral sucker, the muscle-fibres being, if anything, slightly stouter and the myoblasts proportionately less numerous. The sucker as a whole does not project much above the surface of the body.

A word must be said here with regard to the dimensions of the suckers as stated by Olsson. Considerable discrepancy exists, which necessitates an attempt at explanation. The sizes given by Olsson are ·40–·52 mm. for the oral sucker and ·63–·75 mm. for the ventral sucker. These are evidently much in excess of my measurements and cannot apply to a specimen of 3–4 mm. in length. Olsson says they were measured from a "spec. adult," and by this he must understand a specimen of 5–6 mm. in length. On this supposition the oral sucker would be about one eleventh of the body length and the ventral sucker about one eighth. Moreover, on careful measurement of Olsson's figure I find that the suckers are respectively one eleventh and two fifteenths of the body length. According to Linton also the oral sucker is one eleventh and the ventral sucker one eighth. In view of this agreement it may be taken as a distinctive feature of the species that the oral sucker is one twelfth to one eleventh and the ventral sucker one eighth to one seventh of the body length.

The cuticle has a fairly uniform thickness of ·0025–·003 mm.

The musculature of the body conforms to the usual type, with the three subcutaneous layers, circular, longitudinal, and diagonal, and the less organised parenchymatous fibres.

Close underneath the layer of diagonal muscle-fibres lies a layer of what were formerly regarded as cutaneous glands, but which are, according to Bettendorf,[1] the myoblasts of the subcutaneous muscle-fibres. So far as can be gathered, Bettendorf's views have not been completely confirmed, but they are probably correct. At any rate the glandular nature of these cells has never been proved, and from Bettendorf's work they appear to be in intimate connection with the subcutaneous muscle-fibres. These cells, as I have observed them in this species, stain deep blue with hæmalum-eosin and the nuclei are only differentiated by being denser. The cells are rounded in outline with several filaments, and in many cases they appear fused together in groups of two or three,

[1] 'Zool. Jahrbuch. Abth. Anat.,' x, 1897, p. 307.

so that the outlines of the individual cells are lost. These cells certainly do not resemble the large cells (myoblasts) of the suckers, the cell-substance being much denser. They bear more resemblance to the smaller cells of the suckers, but most of all to the circum-œsophageal and vaginal "gland-cells." The glandular nature of these latter cells is again a matter of hypothesis, and their undoubted resemblance to the "subcutaneous glands" strengthens Bettendorf's views as to their myoblastic nature. The same may be said with regard to the cells surrounding the terminal portion of the ductus ejaculatorius in the cirrus pouch. All these cells are easily differentiated from cells of which the glandular function is well established, i.e. prostate gland and shell gland, even by ordinary staining methods.

True cutaneous glands, however, do exist in this species, but they are restricted in extent. They occur in the anterior part of the body only, situated fairly deeply and scattered throughout the region from the pharynx to the intestinal bifurcation. Similar cells (cephalic glands) appear to exist in many other species, but their occurrence has not been universally confirmed. They are not very numerous, but their number could not be estimated. Their ducts can be easily demonstrated, as also the fact that a considerable number of them open around the oral sucker. They are somewhat pear-shaped or tear-shaped, with their narrow end directed forwards. They measure about ·036 by ·019 mm., and their contents consist of a homogeneous, finely granular material, staining light blue with hæmalum-eosin, in the midst of which is a large round nucleus, ·007 mm. in diameter, with distinct nucleolus. The function of these glands is still a matter of opinion. According to Leuckhart and Looss their secretion exercises an irritative action on the tissues of the host, causing an increased flow of juice, and even, according to some authors, a flow of blood in certain cases. This seems a reasonable enough supposition and is supported by the position of the glands. It may also account for the fact that some animals, although harbouring an immense number of

Trematode parasites, do not appear to suffer from their presence, but may indeed possibly benefit by the increased stimulation of the gastric and intestinal glands. An alternative theory with some claim to recognition is that the secretion of these glands renders the contents of the host's intestine less tenacious and thereby facilitates the activity and locomotion of the parasite.

The alimentary system does not offer any striking peculiarity. There is a small pre-pharynx, with thin walls and lined by cuticle continuous with that lining the oral sucker and pharynx. Into this the anterior end of the pharynx projects, so that, on external view, the pharynx appears to be continuous with the oral sucker. In many species the pharynx is described as continuous with the oral sucker, but in most of those it will probably be found that a small pre-pharynx intervenes. One notable exception is Rhytidodes gelatinosus (Rud.), in which no pre-pharynx is present. The pre-pharyngeal vestibule gives the pharynx greater freedom of movement, permitting, as it does, a certain amount of longitudinal movement, independent of the body extension and contraction, while at the same time it allows the anterior end of the pharynx to expand, somewhat after the manner of a sucker. The external membrane of the oral sucker is continued along the pre-pharynx on to the pharynx, which it invests. The pharynx is of moderate size, and nearly globular, but flattened dorso-ventrally. Its diameter is ·15–·19 mm. and thickness ·09–·10 mm. The lumen is a narrow, transverse slit, and the walls are about ·04–·05 mm. thick. The structure is identical with that of the suckers. The radial muscle-fibres have an average thickness of ·0015 mm. and the circular fibres ·001 mm. Towards the anterior end the muscle-fibres are very closely packed. Passing forwards the radial fibres are more and more obliquely set, until they come to run almost parallel to the internal wall. Lacunar spaces are much reduced and cells are rare. Most movement apparently takes place at this part.

The œsophagus is about the same length as the pharynx

(·15–·2 mm.) and the intestinal bifurcation occurs a short distance in front of the ventral sucker. The diverticula are uniform and fairly wide, extending almost to the posterior end of the body. The œsophagus is lined by a somewhat thick membrane (metamorphosed epithelium), the surface of which is thrown into slight folds. This membrane is continuous with the cuticular lining of the pharynx, but is thicker and stains differently. With hæmalum-eosin it takes on a reddish-purple colour, whereas the cuticle is more distinctly blue. The musculature consists of the usual internal annular and external longitudinal layer, the fibres being more or less widely separated according to the degree of contraction. Surrounding the outer layer is a ring of very loose connective tissue, on the outer edge of which are numerous small, blue-staining cells—the myoblasts of the œsophageal muscles. The diverticula separate at a wide angle and bend towards the outer side of the ventral sucker. The rest of their course is practically straight, with a slight turn in near the end. At first they lie midway between the dorsal and ventral surfaces of the body, but on passing the ventral sucker they assume an unvarying dorsal position and are surrounded on all sides except dorsally by the yolk-glands. The average width of each diverticulum is about ·08 mm. Their transverse section appears sometimes oval, sometimes triangular, and sometimes almost circular. The lining consists of a single layer of epithelial cells, with well-marked nuclei and nucleoli. The nuclei measure ·005–·008 mm. The cells are of irregular shape, with long fibrillar or hair-like processes stretching into the lumen and filling it up to some extent. Amidst the cells there are numerous small vacuoles. The appearance presented, in fact, is that of a row of nuclei lying in the midst of a fibrous feltwork; the cell outlines are difficult to distinguish. This epithelial layer is absent in a small part of the diverticula just behind the bifurcation, and is replaced by a continuation of the œsophageal membrane. This recalls the condition in Patagium brachydelphium Heymann, in which the initial part of the diverticula is constricted and devoid of

epithelium. It is thus histologically part of the œsophagus. This condition is of some structural importance. In other species which I have been able to examine, and particularly in the Allocreadiinæ, the layer of epithelial cells is continued right up to the junction with the œsophagus. The musculature of the diverticula is the same as that of the œsophagus, but the fibres are more irregularly spaced.

The excretory vesicle consists of a single undivided terminal sac, lying just under the dorsal surface of the body and extending as far forwards as the anterior border of the anterior testis, where it divides into two much narrower tubules running forwards to the level of the oral sucker. Over the testes the vesicle is compressed transversely, but elsewhere it is nearly isodiametric. The excretory pore is not quite terminal but is displaced very slightly dorsally. In section the wall presents an irregular outline. The lining of the vesicle consists of a distinct but thin membrane, which stains like cuticle, and under this there is a regular layer of oval nuclei with their long axes parallel to the wall of the vesicle. No cell outline could be discriminated. The nuclei possess a distinctive character in the apparent absence of nucleoli. They contain numerous chromatophil threads and granules staining rather dark blue, while the rest of the nucleus has a lighter tint. These nuclei can be traced throughout the greater part of the excretory system and appear to be peculiar to it. This lining membrane evidently does not conform to the usual type, in which the epithelial cells are prominent in the wall of the vesicle and are sharply marked off from the surrounding tissues. Here the cells are not prominent, and they are in close relation to the adjoining parenchyma.

Genital system: The testes are two rounded or ovoid bodies, situated directly behind each other in the middle line of the body. The posterior testis is about one quarter of the body length from the posterior end, while the anterior testis is separated from the ventral sucker by a shorter space. They may be closely apposed to each other, or more usually

separated by a narrow space occupied by yolk-glands. Their outline is slightly irregular, but not lobed. The anterior testis is often hollowed out in front and transversely elongated; it varies in size and shape much more than the posterior testis does. The antero-posterior axis measures ·21–·28 mm., the transverse axis ·26–·44 mm. The corresponding measurements of the posterior testis are ·28–·43 mm and ·29–·39 mm. The average is about ·27 by ·34 mm. for the anterior, and ·34 by ·33 mm. for the posterior. Thus the diameter is rather less than one tenth of the body length. This result is in close agreement with the figures of Olsson and Linton. Olsson, however, states that the testis exceeded the ventral sucker in size. That was certainly never the case in any of my specimens, nor does it appear to be so from Linton's figure.

There is no sinus genitalis, or at most it is represented merely by a shallow depression, in which the male and female ducts open separately but contiguously, the former in front and to the left of the latter. In total preparations, however, only one aperture is sometimes seen. Its position is invariably median and exactly ventral to the posterior end of the pharynx. In Olsson's representation of the species (Pl. IV, fig. 52) the apertures are shown widely separate, but this is evidently the result of an erroneous observation, which I shall endeavour to make clear. The apertures are figured behind the intestinal bifurcation, between it and the ventral sucker, and they appear to be separated by a distance of nearly ·2 mm. Further, from the supposed male aperture a long penis is represented stretching straight forwards to about the middle of the pharynx, while the cirrus-pouch shows a somewhat elongated oval outline quite different from the pear shape of my specimens. To me it appears that the structures marked *p* and *b* in fig. 52 are really portions of the cirrus-pouch, *b* being the thicker posterior part and *p* the narrow anterior part or neck running forward to the genital aperture near the posterior end of the pharynx. The erroneous position of the female genital aperture is probably due to the fact that

Olsson mistook the point beyond which the ova could not be seen for the termination of the vagina—a not at all unlikely mistake. On such a supposition my specimens agree very well with those of Olsson, otherwise the difference is of more than specific value.[1] On this matter Linton says nothing definite, but his figures show the genital aperture well forward in the neck, always single and sometimes with exserted cirrus. Careful measurements of his drawings, which we may assume to be drawn in proportion, show that the genital aperture is nearer to the posterior end of the pharynx than to the anterior border of the ventral sucker. In fig. 30, where the pharynx is not represented, the genital aperture is about ·19 mm. behind the posterior border of the oral sucker. The average length of the pharynx being ·16 mm. it is evident that the genital aperture is not far behind its posterior border.

The fact that Linton represents the genital aperture single tends to cast some doubt on my observation of the absence of a sinus genitalis. The exserted cirrus in Linton's specimens might have obscured the double aperture, but it is possible that the condition as I observed it was purely accidental. Against this is the fact that it occurred in several specimens.

The cirrus-pouch is, as already mentioned, of the characteristic Distomid shape, with a wide posterior part containing the vesicula seminalis, gradually narrowing into a slender anterior part containing the terminal part of the ductus ejaculatorius. The latter usually passes straight back from the genital aperture, and the thicker part is bent on it either to the left or to the right. It extends back to the level of the centre of the ventral sucker. It occasionally does not

[1] By the kindness of Dr. Jägerskiöld I have been enabled to examine two of Olsson's original specimens from Thymallus vulgaris and to confirm the correctness of the above suppositions. The genital aperture (or closely apposed apertures) is situated midway between the two suckers and therefore not far behind the end of the pharynx. Its position is probably most correctly described as midway between the suckers.

reach this level, but seldom, if ever, exceeds it. Its length is ·45–·55 mm.; the maximum diameter is ·12 mm., and the average diameter of the neck is ·05 mm.

The pouch is a true muscular cirrus-pouch, and its wall consists of the frequently described internal annular layer and external longitudinal layer. It thus differs essentially from that of Bunodera nodulosa (Zed.), in which the wall is purely membranous.

The structures contained within the cirrus-pouch conform to the common type, e. g. that of the Allocreadiinæ, but they are simple and less complicated. The vesicula seminalis is an undivided elongated oval sac (fig. 3), measuring ·2 by ·04 mm. It is not in the slightest degree convoluted. It is surrounded on all sides by the cells of the prostate glands, except towards the posterior end, where it is contiguous with the wall of the cirrus-pouch. The length of the ductus between the vesicula and the pars prostatica is about ·15 mm. For the first two thirds of that length it has a diameter of ·015 mm.; it then somewhat suddenly widens to ·023 mm., which diameter it retains till it passes into the pars prostatica. The latter has a length of ·05 mm., and a maximum diameter of ·035 mm. It has a globose shape, and into it open the ducts of the numerous prostatic cells. These are entirely confined to the part of the cirrus-pouch behind the pars prostatica, so that their ducts all pass forward. They are large tear-shaped cells elongated in the long axis of the cirrus-pouch, and having an average size of ·027 by ·012 mm. Their outline may be more or less quadrilateral owing to compression. They stain deep purple with hæmalum-eosin, and have distinct round, rather small (·004–·005) nuclei. The terminal part of the ductus ejaculatorius, which, although not extended in any of my specimens, functions as an ex-sertile cirrus, is slightly convoluted. As a rule it describes only one turn, a little in front of the pars prostatica, but its position is not constant. The length of this part is about ·1 mm. and its diameter is ·02–·025 mm. Between this part and the wall of the cirrus-pouch are numerous small, round cells.

These are obviously not prostatic cells, for they present a different appearance and take on a distinctly blue stain. Moreover, ducts cannot be made out. Various functions have been ascribed to these cells. Most frequently they have either not been noted or considered to be prostatic cells. They have also been regarded as glands opening into the ductus ejaculatorius. Neither of these theories has been verified. The staining reaction differentiates them from the prostate cells and from similar cells, e.g. those of the shell-gland. On the other hand, they bear a distinct resemblance to the circum-œsophageal and peri-vaginal cells, as also to the "subcutaneous gland cells" (i.e. myoblasts). The resemblance to the circum-œsophageal cells, which Bettendorf[1] has shown to be the myoblasts of the œsophageal muscle-fibres, suggests that the cells surrounding the ductus ejaculatorius, as also the peri-vaginal cells, are the myoblasts of the muscle-fibres of the walls of these structures.

The ovary is an almost globular body situated close behind the ventral sucker and a considerable distance in front of the anterior testis. It may lie on either side of the middle line, or, according to Olsson, it may be median. In none of my specimens did it occur in the latter position; it was most frequently on the left side. The size is ·23 by ·19 mm., the thickness ·16 mm. The configuration of the shell-gland complex has already been carefully described by Blanchard. Just behind the ovary lies a small oval receptaculum seminis. From its inner side there arises a duct giving off Laurer's canal, which is a straight tube of moderate length, and then running forwards to join the oviduct. The latter issues from the inner surface of the ovary, and passes backwards. After being joined by the duct from the receptaculum seminis, it turns forwards to pass into the ootype, and thence into the uterus. Blanchard's representation of the shell-gland is somewhat diagrammatic. It is much more extensive and is not enclosed within a membrane. It lies under the dorsal

[1] "Über Muskulatur und Sinnezellen der Trematoden." 'Zool. Jahrb. Anat.,' x (1897).

surface of the body, and consists of a large number of small cells closely aggregated and composing a fairly distinct body to external view.

The common yolk-duct joins the oviduct between the entrance of the ductus receptaculi and the ootype. The yolk reservoir lies just behind the shell-gland and is median. It forms a more definite swelling than Blanchard indicates. It is formed by the junction of the two transverse yolk-ducts. The longitudinal ducts run parallel to the intestinal diverticula and along their ventral surface. The yolk-glands consist of two lateral groups of follicles extending continuously from the level of the pharynx to the posterior end of the body. Behind the posterior testis they extend in towards the middle line and fill up the posterior part of the body. In addition offshoots are sent in between the testes and in front of the anterior testis, and these almost unite in the middle line, thus separating the testes from each other and from the uterus. There is no tendency towards proliferation in front of the ventral sucker, the lateral fringes having a fairly constant width. Their situation is particularly towards the ventral surface, so that laterally they lie ventral to the intestinal diverticula and posteriorly they do not approach the dorsal surface to any great extent. The follicles are irregularly ovoid and measure ·08–·10 by ·04–·06 mm. Each contains about a dozen gland cells, which present two distinct appearances. In each follicle there is almost invariably one cell situated centrally (fig. 4) differing from the surrounding cells in shape and staining reaction. This central cell appears to be free, not much compressed by the neighbouring cells, and in consequence has a regular oval outline. The remaining cells are closely pressed together into various polyhedral shapes. The staining reaction is more distinctive. The stain used was weak hæmalum with aqueous eosin, but corresponding results were obtained with combinations of hæmatoxylin, methylene blue, and saffranin. The peripheral cells take on a uniform purple colour, while the central cell appears pink with a circumferential granular zone. The nuclei

also differ. In the peripheral cells they appear to consist of three concentric layers. The outmost zone is granular and stains deep blue, the middle is white, while the central part, the nucleolus, stains bright red. In the central cell, on the other hand, the nucleus stains uniformly bright red and appears to consist of little more than the nucleolus. The cells measure ·02–·03 mm. in diameter, while the nuclei measure ·006–·0075 mm., but those of the peripheral cells appear to be slightly larger than that of the central cell. The central cell is obviously the most mature part of the follicle, and it is probable that only in this condition are the yolk-cells despatched from the follicles. The yolk-ducts and reservoir, at any rate, contain only such cells. In their passage down the yolk-ducts they are compressed into a cubical or short cylindrical shape; in the reservoir they become polyhedral, but they again become cubical on passing into the common yolk-duct. They retain their bright red nuclei throughout, and these are still conspicuous within the most mature ova. No intrinsic muscle-fibres or true epithelium of the yolk-follicles or yolk-ducts could be observed, but this does not prove their absence as they are particularly difficult to demonstrate.

Turning back from the ootype the uterus describes a moderate number of convolutions in the space between the posterior border of the ventral sucker and the anterior border of the anterior testis. Laterally it is confined by the intestinal diverticula. Owing to its thickness the ovary is not overlapped by the uterus. The convolutions tend towards and cause bulging of the ventral surface of the body. The terminal part of the uterus runs straight forward on the right side of the cirrus-pouch and passes into the vagina at the level of the posterior end of the pouch. The vagina is also straight and has the usual muscular structure. Its diameter is ·019 mm. in the undilated condition. The cuticular lining is ·004 mm. thick. The thickness of the combined muscular layers is ·003 mm. and the diameter of the lumen is only ·005 mm. To admit the passage of the ova it

must therefore be capable of considerable dilatation It is surrounded by lax connective tissue, in which are embedded the peri-vaginal cells already referred to.

The ova are usually less than 100 in number. The shape is ovoid, slightly blunter at the opercular pole. The shell is ·0018 mm. thick and bright yellow, not darkening much throughout the uterus. The size of the ova is ·075–·080 by ·040–·044 mm.; this is somewhat larger than the size quoted by Olsson, but agrees closely with that of Linton. There is absolutely no intra-uterine segmentation, the ovarian ovum remaining undivided till deposition. The yolk-cells within the egg also remain unchanged, and can be easily distinguished from the ovarian cell by their bright red nuclei, the nucleus of the ovarian cell taking on a darker, nearly purple colour with hæmalum-eosin.

Olsson's figure (Pl. IV, fig. 52) gives a somewhat erroneous impression of the appearance of the ova and uterus in a specimen of average size. The ova are usually proportionately larger and the convolutions of the uterus are indistinguishable.[1]

Systematic position of Distomum laureatum Zeder.

The inclusion of this species within the sub-genus Crossodera by Dujardin in 1845 need not be discussed here. The most recent attempt to define its systematic position is that by Braun,[2] and his classification is accepted by Looss,[3] Heymann,[4] Pratt[5] and Stafford[6]. Braun included it in a new genus, Crepidostomum, of which the type is C. metœcus (Brn.) from bats. The two species are certainly very nearly

[1] In the two specimens from Olsson's collection which I examined the uterus does not have the disposition represented by Olsson. The ova are congregated more over the dorsal surface of the ventral sucker, so that they are best seen on viewing the animal from the dorsal surface.

[2] 'Annal Hofmuseum, Wien,' xv (1900), p. 232.

[3] 'Zool. Jahrb. Abth. Syst.,' xvi (1902), p. 453.

[4] 'Ibid.,' xxii (1905), p. 97.

[5] 'American Naturalist,' xxxvi, p. 957.

[6] 'Zool. Anzeiger,' xxvii, p. 490.

related, but in my opinion D. laureatum does not belong to the genus of which D. metœcus is the type. The widely different hosts might in the first place raise doubt as to the close relationship of the two forms, although, as Braun remarks, too great weight need not be attached to this, because the larval stages of both may be passed through in insect larvæ forming food common to bats and fishes. We may therefore neglect this.

The close resemblance between the two species, however, is not borne out on more detailed examination. Several important features of difference are apparent. The first, and possibly the chief of these, is the condition of the circum-oral swelling and papillæ. Braun did not fail to notice the difference here, but he under-estimated its importance. In Crepidostomum metœcus the circum-oral collar is confined almost entirely to the dorsal surface of the sucker. It does not extend on to the ventral surface, and thus its edges are at some distance from the aperture of the sucker. In Dist. laureatum the collar completely encircles the sucker and its edges are contiguous with, or even project into, the apertnre. There are thus no ventral papillæ in C. metœcus, all being dorsal, or at most two being dorso-lateral. Further, they are only five in number as opposed to six in D. laureatum. Braun's attempt to correlate the discrepancy is certainly ingenious, and possibly explains to some extent the origin of the papillæ and the increase in their number. He considers that the median dorsal papilla in C. metœcus which is furcate (zweizipfelig), must be regarded as a double papilla, and as such is equivalent to the two dorsal papillæ of D. laureatum. The division of this median papilla would certainly make the number six, but unfortunately Braun ignores the fact that (from his own description, p. 230) the two neighbouring papillæ are not altogether simple, but appear to approach the middle papilla in shape, i. e. to be two-pointed or bi-partite. These have equal claim to be regarded as "Doppelpapillen," and in this way the number would be eight. There is no evidence of such splitting of

the papillæ in Dist. laureatum. On the strength of the foregoing alone I should be inclined to exclude Dist. laureatum from the genus Crepidostomum, for it is obvious that there is a wide interval of development between a condition of six and a corresponding condition of five papillæ, even although one or more of the latter is in the process of division. Further differences of generic importance are, however, not difficult to seek. The first of these is to be found in the position of the genital aperture. In Braun's figure it appears midway between the ventral sucker and the pharynx, and he describes it as close in front of the anterior border of the sucker. It is therefore considerably further back than in Dist. laureatum.[1] It appears single in Braun's figure. The cirrus-pouch is of great length, extending beyond the ventral sucker by nearly half the diameter of the latter. In Dist. laureatum it barely reaches the centre of the sucker. Braun does not offer any details of the internal structure of the pouch. A noticeable feature in Crepidostomum metœcus is the enormous size of the testes, each being much larger than the ventral sucker, and their approximation to the posterior end of the body. This cannot be regarded as of very great importance. Of greater moment is the position of the ovary and the condition of the uterus. In Crepid. metœcus the ovary lies not far in front of the anterior testis, on the right side of the body and separated from the ventral sucker by the cirrus-pouch. Braun makes no mention of amphitypy, although he had numerous specimens. The uterus is practically minimal in length and contains not more than two or three ova, which are much smaller (·055 mm.) and broader than those of D. laureatum. Other features of difference are the nearly equal suckers, the somewhat small, round ventral sucker, and the absence of pre-pharynx and œsophagus in Crepido-

[1] I may be here accused of inconsistency in admitting the correctness of Braun's observation while doubting that of Olsson; but the justification lies in the fact that many errors have been found throughout Olsson's work, whereas Braun's observations are, as a rule, beyond dispute.

stomum metœcus, but the last mentioned is of little importance, for, as Braun remarked, a short œsophagus may be present as also a pre-pharynx.

The features of primary diagnostic importance are, therefore, the circum-oral collar and papillæ, the position of the genital aperture, the length of the cirrus-pouch, and the extent of the uterus with the number and size of the ova; of secondary importance are the large testes, the nearly equal suckers, and possibly the position of the ovary in Crepid. metœcus. That these are of much greater than merely specific importance can hardly be denied, and it follows that Dist. laureatum Zed., cannot be included in the genus Crepidostomum Braun. From the genus Acrodactyla Stafford[1] it differs in having the ventral sucker considerably larger than the oral sucker, the rather short cirrus-pouch, and apparently the ventral papillæ not so pronounced. The structure of the cirrus-pouch in Acrodactyla is not mentioned, but it is presumably muscular. From the genera Bunodera Raill. and Patagium Heymann it is sufficiently distinguished by the structure of the cirrus-pouch, the extent of the uterus, and other features to which I shall refer later. In short, it must be regarded as the type of a distinct genus, for which I propose the name Stephanophiala, with the following provisional definition:

Body of medium size, elongated, flattened. Cuticle unarmed. Suckers fairly muscular, the ventral sucker being larger than the oral sucker, and situated on the border of the first and second thirds of the body-length. Oral sucker subterminal, with its anterior part swollen and surrounded by a row of six equal, muscular, contractile papillæ, arising from the muscle-substance of the sucker, two being ventral and four dorsal. Intestine with short pre-pharynx, medium-sized pharynx, short œsophagus, and diverticula extending to hind end of body. Excretory vesicle simple. Genital aperture median, midway between suckers. Sinus genitalis absent or rudimentary. Cirrus-pouch with muscular walls

[1] 'Zool. Anzeiger,' xxvii, p. 491.

not extending much, if at all, beyond the ventral sucker. Vesicula seminalis simple; ductus ejaculatorius only slightly convoluted; distinct pars prostatica; prostatic cells fairly numerous. Vagina of no great length. Testes, two, rounded, close behind each other, about midway between ventral sucker and posterior end of body. Ovary rounded, not far behind ventral sucker, and separated from the testes by part of the uterus, which is of moderate length, confined between ventral sucker and anterior testis. Yolk-glands lateral, extending nearly the whole length of the body and uniting behind testes. Receptaculum seminis and Laurer's canal present. Ova not very numerous, measuring about ·075 × ·04 mm. No intra-uterine segmentation.

Type: St. Laureata (Zeder). Includes also St. transmarina n. sp. [= Crepidostomum laureatum (Zed.) Stafford, 1904], and probably two other undescribed American forms (see p. 35).

With regard to the systematic position of the genus it probably lies nearer Acrodactyla than Crepidostomum. From Bunodera, Patagium, Rhytidodes and others it is much further removed. Heymann has already discussed the relationship of the genus Crepidostomum to Bunodera and Patagium. The somewhat scanty knowledge of the first-named genus did not appear to offer any serious obstacle to the inclusion of these three genera under the subfamily Bunoderinæ, and, in addition, the importance of the recognised features of difference was under-estimated, as will be evident from what follows.

The presence of circum-oral swellings or papillæ being a rare and peculiar occurrence amongst Distomids, the most natural conclusion is that they must have been evolved from some simpler type. That they bear no analogy to the much commoner collar of cephalic spines of the Echinostominæ and other forms has already been amply demonstrated by Looss, and needs no further discussion here. The resemblance, however, in the internal anatomy of the genera under consideration, especially of Stephanophiala, to the Allo-

CREADIINÆ and allied forms has previously been remarked on by more than one author, and there is certainly no other known group to which they seem so closely connected. Bunódera and Patagium, nevertheless, diverge widely from the ALLOCREADIINÆ in several respects. On the other hand, were it not for the circum-oral papillæ, Stephanophiala laureata might be regarded as an Allocread.

From the point of view of the circum-oral collar, the genera Patagium and Rhytidodes Lss. show the most primitive condition of a simple swelling of the muscle-substance of the sucker with commencing differentiation. The next stage, considerably removed, is that of Crepidostomum in which papillæ have appeared, showing a tendency to further subdivision, and the most advanced stage is that of Stephanophiala, Bunodera and Acrodactyla, in each of which the condition is very similar, although, as I have tried to show, they may not be the direct evolutionary products of forms such as Crepidostomum, but may have proceeded along independent lines, the intermediate members of which have been lost or are not yet known. A consideration of the internal anatomy leaves hardly a doubt of this, for Stephanophiala and Bunodera differ very much, while the former approaches Crepidostomum and the latter Patagium.

From a detailed examination of the internal structures it is evident that Stephanophiala closely resembles the ALLOCREADIINÆ in its most essential features, viz. the position of the genital aperture, the structure of the cirrus-pouch and its contents, the position of the testes, the extent and situation of the uterus, and the condition, size and number of the ova. This appears to have been noticed by Pratt[1] who included Crepidostomum Brn. in a sub-family, PSILOSTOMINÆ Pratt, comprising Allocreadium and several allied genera,[2] while

[1] 'American Naturalist,' xxxvi, p. 888.

[2] Pratt is rather inconsistent, for on p. 896 he notes: "Yolk-glands do not extend in front of acetabulum" as a feature of the sub-family PSILOSTOMINÆ, while just above he has—"Yolk-glands extend in front of acetabulum," under which sub-division he puts Calycodes Les.,

Bunodera is relegated to a separate sub-family, Bunoderinæ Pratt, including the rather anomalous genus Tergestia Stoss.

In Crepidostomum the uterus appears to have undergone a process of retrogression or degeneration, while Bunodera, and, to a less degree, Patagium display a condition altogether foreign to the Allocreadiinæ, in which the uterus never extends beyond the anterior border of the first testis. In Crepidostomum and Acrodactyla the structure of the cirrus-pouch is not well known, but indications point to its being not unlike that of Stephanophiala. Bunodera and Patagium again display a distinctly different type, with non-muscular wall and more or less highly-convoluted vesicula seminalis. The absence of muscle-fibres might be regarded as the result of a series of degenerative changes, but that is merely hypothetical. Further, in Bunodera the condition of the ova, in which a Miracidium larva is developed within the uterus, is very dissimilar from that of the Allocreadiinæ and Stephanophiala. In Crepidostomum and Patagium the condition of the ova is not known.

The inclusion, therefore, of all these genera within the sub-family, Bunoderinæ, as proposed by Looss and Heymann, is not without objection. They are possibly related, but how closely is not very apparent. Too great weight has hitherto been placed on their common possession of a circum-oral collar, and, as in the case of Rhytidodes, such a structure may be present in a genus which cannot be included in the same sub-family. To consider the circum-oral collar as the diagnostic feature of the sub-family Bunoderinæ would be a reversion to the now discarded system of classification by external characters. We must therefore look to the internal structure, mainly, for guidance. From this it is evident

Crepidostomum Brn. and Helicometra Odhn., although he includes those genera in his sub-family. Pratt's classification is obviously premature but it is of great help, and he is certainly correct in separating Bunodera from the Psilostominæ.

that a somewhat broad line of separation exists between Stephanophiala, Acrodactyla and Crepidostomum on the one hand and Bunodera and Patagium on the other. It is unfortunate that more details are not available in the case of Crepidostomum, Acrodactyla, and Patagium, but from what is actually known it is highly probable that they display all the features mentioned in the following table:

	Stephanophiala (Crepidostomum and Acrodactyla?).	Bunodera (and Patagium).
1. Testes	Directly tandem	Oblique
2. Uterus	Confined between ventral sucker and anterior testis	Extending beyond testes, and even filling up posterior part of body.
3. Cirrus-pouch	Muscular; vesicula seminalis and ductus only slightly convoluted	Membranous (non-muscular); vesicula and ductus highly convoluted.
4. Ova	No intra-uterine segmentation	Miracidium larva developed within uterus.

The difficulty again arises as to the precise importance to be attached to these differences in structure. From a study of the methods of classification propounded and developed by Looss I take it that the condition of the ova and the cirrus-pouch are of extreme importance, and that genera differing in two such essential features can hardly be included in the same sub-family. On examination of already existing and strictly demarcated sub-families it will be found that no such divergence in structure is to be met with. Amongst such sub-families, for example, as the Echinostominæ, Allocreadiinæ or Gorgoderinæ with their comparatively numerous members no such difference in structure would be admitted. From these considerations, therefore, it seems advisable to separate the genera Stephanophiala and Crepidostomum from the sub-family Bunoderinæ,

and to establish for them a distinct sub-family for which I propose the name Stephanophialinæ n. subfam., with the following provisional diagnosis.

Small to under middle-sized forms with fairly muscular body, the anterior part of which is capable of considerable extension. Cuticle without spines or scales. Suckers muscular and of moderate size, the ventral sucker being situated at the end of the anterior third of the body or somewhat further back. Oral sucker with a circum-oral collar developed from the muscle substance of the sucker, from which a number (five or six) of small tentacular papillæ arise. Intestine with very short pre-pharynx, muscular pharynx, short œsophagus, and long simple diverticula extending to posterior end of body. Genital aperture median, between the suckers. Sinus genitalis small or vestigial. Cirrus-pouch elongated, with muscular walls. Vesicula seminalis and ductus ejaculatorius simple and not much convoluted. Testes two, simple, median in the middle of the post-acetabular region. Ovary simple, rounded, not far behind ventral sucker and separated from testis by part of uterus. Receptaculum seminis and Laurer's canal present. Yolk-glands mainly lateral, extensive. Uterus confined between anterior testis and ventral sucker. Vagina simple, short. Ova not numerous, measuring about ·05–·08 mm. No intra-uterine segmentation.

Type: Stephanophiala Mihi. Including also probably Crepidostomum Brn., and very doubtfully Acrodactyla Stafford.

As a result of this separation Heymann's definition of the sub-family Bunoderinæ Lss. requires modification. The sub-family must for the present be restricted to the genera Bunodera and Patagium, and it is obvious that these genera differ from each other much more than Crepidostomum and Acrodactyla do from Stephanophiala, not only as regards the circum-oral collar but also in respect of the internal structure. The modifications, as already indicated, are: Suckers nearly equal; testes oblique; uterus extending

beyond the testes; terminal part of male genital apparatus enclosed within a non-muscular pouch; vesicula seminalis convoluted; ovary immediately behind ventral sucker and separated from testes by considerable part of uterus; ova contain a Miracidium larva before deposition. Length ·08–·10 mm.

Type: Bunodera Raill.

In addition to the species hitherto mentioned there are several other forms, mostly from America, which possess a row of circum-oral papillæ. Two of those, Distomum auriculatum Wedl. and D. petalosum Lander, were regarded by Looss[1] as probable members of the genus Bunodera Stafford,[2] however, differentiated D. petalosum Lander (= D. auriculatum Wedl. Linton) from Bunodera, and proposed it as type of the new genus Acrodactyla. The chief features of this genus, according to Stafford, are the large ventral oral papillæ, the position of the genital aperture, and the large cirrus-pouch. To these I should add the fact that the ventral sucker is smaller than the oral. The structure of the cirrus-pouch and the condition of the ova are not noted. The limited extent of the uterus indicates that this genus is more nearly related to Stephanophiala and Crepidostomum than to Bunodera, and I have included it provisionally within the sub-family Stephanophialinæ.

With regard to the American forms of Distomum laureatum described by Linton and Stafford, it is doubtful if they are really identical with the European variety. The only differences which I can detect in Linton's specimens are the backward position of the ovary and the slightly reduced number of ova. In Olsson's figure of the species, however, the ovary is a little distance behind the ventral sucker, so that this variation may occur in the European form. The smaller number of ova may be only a seasonal variation. Linton makes no mention of the cirrus-pouch, but Stafford says it

[1] 'Zool. Jahrb. Syst.,' xvi. p. 453.

[2] 'Zool. Anzeiger' (1904). xxvi. p. 491.

extends beyond the ventral sucker. The latter also describes the ovary as midway between ventral sucker and anterior testis, and the ova as not numerous—ten to twenty. In this case it is apparent that a different species is under consideration, for in the European form, according to Olsson's observation, which I confirm, the cirrus-pouch does not extend beyond the centre of the ventral sucker. For this American species I propose the name Stephanophiala transmarina (= Crepidostomum laureatum Stafford, 1904, = ? Distomum laureatum Linton, 1893) from Salvelinus fontinalis Mit. and Salmo mykiss.

Stafford mentions two other varieties, one from Perea flavescens, the other from Necturus maculatus, and these will possibly prove to be further species of the genus Stephanophiala. With regard to Crepidostomum cornutum (Osborn),[1] it is doubtful if this species can be included in the genus Stephanophiala. The small size of the ventral sucker is against this and brings it into closer relation with Acrodactyla. The species, however, is not yet sufficiently well known for its position to be determined. If it cannot be included in the genus Acrodactyla it may require to be considered as the type of a distinct genus.

The natural sequel to the foregoing classification would be the formation of a family Bunoderidæ along the lines indicated by Heymann in his definition of the sub-family Bunoderinæ, but such a step would be undoubtedly premature, if not erroneous. It must be regarded as very doubtful if the Stephanophialinæ are so closely related to the Bunoderinæ, as has been hitherto considered. Most indications seem to point to a further separation of these two sub-families, and a nearer approximation of the Stephanophialinæ to the Allocreadiinæ. This, however, must be a matter for future determination.

[1] 'Science,' xv (1902), p. 573.

Sub-family Brachycladiinæ Odh., 1904.

Genus Brachycladium Lss., 1899.

Brachycladium oblongum (Braun). Pl. 9, figs. 6—9.

? = Campula oblonga Cobbold.

1900. Campula oblonga Cobb. Braun, 'Centralbl. f. Bakter.,' xxviii; 'Abtheil.,' i, pp. 249–255, 3 figs.

1902. Brachycladium oblongum (Brn.), Looss, 'Zool. Jahrb. Abth. Syst.,' xvi, pp. 707–717 and 775–778.

1904. Brachycladium oblongum Odhner, 'Die Trematoden des arktischen Gebietes, Fauna Arctica,' iv, p. 347.

This species has been the cause of much systematic discussion, and its ultimate fate may be regarded as a critical test of the priority law as applied to zoological nomenclature. The root of the trouble lies in the fact that Cobbold's type specimens of Campula oblonga have been lost or destroyed, and that his description[1] of the species is inadequate to differentiate it from allied and more recently discovered species. I have made an exhaustive but fruitless search for Cobbold's specimens, and it may certainly be considered that they no longer exist, unless, perchance, in some private collection. What remains to us, therefore, of Cobbold's species is merely his scanty description, which, as Looss justly remarks, is of no value whatsoever for diagnostic purposes. Braun's identification, as Campula oblonga Cobb., of a species which he found in the same situation in the same host as Cobbold found his specimens, is regarded by Looss as inadmissible, and his opinion is seconded by Odhner. Braun defended his diagnosis on the ground of the similarity of habitat and the manifest resemblance between his specimens and Cobbold's description and figure so far as they went, but Looss pointed out that Brachycladium palliatum Lss., Br. rochebruni Poir., and Br. delphini Poir. resemble Cobbold's Campula oblonga just as closely as do Braun's specimens, and so might just as readily be

[1] 'Trans. Linn. Soc. Lond.,' xxii (1858), p. 168, Pl. XXXIII, figs. 84, 85.

regarded as Campula oblonga. The obvious outcome of this is that Campula oblonga Cobbold must be considered a nomen nudum, and that Braun's specimens must be re-named Brachycladium oblongum (Braun). I am able to offer a justification, in part, of Looss's conclusions, for in a female porpoise which I have recently (August, 1908) examined I found in the bile-ducts, in addition to numerous examples of Brachycladium oblongum (Brn.), a single specimen of another Trematode. This was accidentally discovered on washing the parasites, and, in spite of further repeated search no more specimens could be obtained. It was easily differentiated from Brachycladium oblongum by its deep red colour, more elongated body, and the apparent absence of spines. I have not yet identified this specimen, but it appears to be a species of Brachycladium. This species could not possibly have been the one Cobbold found, but its occurrence shows that more than one Trematode species may have as its habitat the bile-ducts of Phocæna communis.

The first specimens which I had the opportunity of examining formed part of Professor McIntosh's collection, and were obtained by him from the liver of a porpoise shot in Lochmaddy (North-West of Scotland) in April, 1865. About fifty examples were found, and they were identified by Professor McIntosh at that time as Campula oblonga Cobbold. As already mentioned I have obtained the same parasite myself from one of two porpoises captured in the Firth of Clyde, near Millport. The first of these, a young male, was unaffected, but in the second, one of the lobes of the liver contained more than a hundred specimens. The presence of the parasites in the liver was indicated by large yellowish prominences on its surface, which felt extremely hard. The same stony hardness could be felt throughout the substance of the affected lobe. On opening into it the biliary canals were found lined with a thick layer of dense fibrous tissue. The terminal parts of the canals were usually dilated to form small sacs, in which large numbers of the parasite were closely packed together. These were, however, easily pressed out. Detailed examination has

shown these specimens to be identical with the species described by Braun, or, at most, to differ very slightly from it. Braun's description deals only with the more obvious anatomical features, and I propose here to describe the structure in fuller detail. Looss has already [1] given a fairly exhaustive account of the anatomy of Brachycladium palliatum, and it may be of interest to see in how far his results are borne out by my observations.

The specimens obtained from Lochmaddy were well preserved in alcohol and most of them were in a moderate state of extension, although few were so greatly extended as the specimen shown in Braun's fig. 3. The most general length was 5–6 mm., and the breadth of the specimens was 2–2·5 mm., i. e. the length is about two and a half times the breadth. My own specimens are more extended. Many of them reached 7 mm. in length, and the length was three to three and a half times the breadth. This agrees with Braun's observations.

The other Brachycladium spp. are much more elongated than this, the length being in the case of Br. rochebruni ten times the breadth, while in Br. palliatum it is five or six times. The greatest thickness in my specimens was ·75–·85 mm. The outline is broadly lanceolate, being somewhat pointed at each end. The greatest breadth occurs just behind the ventral sucker, the greatest thickness at the level of the genital aperture.

The whole body is covered with a thick cuticle, varying from ·008–·013 mm. in thickness, but not in any uniform manner, thicker and thinner parts alternating with each other, and there being no difference in this respect between ventral and dorsal surfaces. The cuticle is much thinner than that of Br. palliatum. Strong spines stud the entire surface of the body, being present right to the posterior end, and even in a small depression on which the excretory vesicle opens. As usual they vary much in size, the largest spines being found about the thickest part of the body and the size gradu-

[1] 'Beiträge z. Kenntnis der Trematoden. Zeitschr. f. wissen. Zoolog.,' xli (1885), pp. 390–427, figs. 1–14 and 30.

ally diminishing forwards and backwards. Around the oral sucker they are ·019 mm. long with a base measurement of ·0045 mm. The maximum size about the middle of the body is ·058 by ·014 mm. Towards the posterior end they measure ·037 by ·012 mm. They are thus much shorter than the spines of Br. palliatum. The spines are deeply embedded in the cuticle, penetrating its whole thickness and causing bulging of the basement membrane. Immediately beneath the latter lie the usual three layers of muscle-fibres. The circular fibres have a diameter of ·0019 mm., and are separated by spaces equal to their diameter. The longitudinal fibres measure ·003–·004 mm., and are separated by spaces of ·006–·01 mm. The diagonal fibres measure ·0035–·0055 mm., and are widely separated by spaces of ·04 mm. Those passing in opposite directions make an angle of 125° with each other, but this varies with the state of contraction. The longitudinal and diagonal fibres run for the most part in pairs, which are in more or less intimate contact. Sometimes they are indistinguishable; sometimes a distinct interval separates them. This corresponds with the condition described by Looss in Br. palliatum. In both species the circular fibres run singly.

The suckers are small in comparison with the size of the animal. Both are globular with circular apertures, and present no peculiar feature. The oral sucker is subterminal and has a diameter of ·33 mm. The ventral sucker is situated at a distance of rather more than a quarter of the body length from the anterior end, and has a diameter of ·43–·46 mm. The diameters are therefore in the proportion of 3 : 4, and are respectively about one sixteenth and one twelfth of the body length (taking the average as 5·5 mm.). This agrees fairly well with Braun's measurements.

The radial fibres of the oral sucker are ·015 mm. thick; those of the ventral sucker ·025 mm., the circular fibres about ·019 mm. The wall of the oral sucker has a thickness of ·078 mm., that of the ventral sucker ·09 mm. The cuticular lining of the suckers is thinner than the cuticle covering the body, being only about ·004 mm. thick.

The mouth opens into a short but wide pre-pharynx. From the ventral side of this there arises a well-marked pre-pharyngeal diverticulum (fig. 8), which passes backwards ventral to the pharynx, and may extend a short distance beyond it. This diverticulum forms part of the pre-pharynx and there is no difference in its structure; its occurrence, however, is constant. Such a structure appears to be absent in Br. palliatum, and was not observed by Braun or Poirier. Its function is not very apparent, but it is a curious fact that in each of three specimens which I examined a number of ova were found in the diverticulum. Ova, however, were found in one case in the intestinal diverticula, and were probably accidentally swallowed. The width of this pre-pharyngeal pouch is ·13–·18 mm., but at its junction with the pre-pharynx it is only ·09 mm. Its walls are in some cases thrown into irregular folds, but they are not muscular.

The pharynx is somewhat flask-shaped, narrowest in front and with its anterior end projecting far into the pre-pharynx. The extreme freedom of movement of the pharynx is evident from the fact that its anterior end may be found directed ventrally, dorsally or towards either side. Its length in a 5·5 mm. specimen is ·36 mm.; breadth ·22 mm. and thickness 20 mm. It is, therefore, a comparatively large structure, and is narrower than that of Br. palliatum and larger in proportion to the size of the animal. The histological structure is the same as that of the suckers. The myoblasts measure ·008–·011 mm., with minute reddish eccentric nucleoli.

The œsophagus arises from the posterior end of the pharynx as a narrow tube, transversely oval in section, with a diameter of ·10 mm. It gradually increases in diameter to ·13 mm., where, at a distance of ·05 mm. behind the pharynx, there is a small dilatation on the left which causes the width to increase to ·20 mm. The bifucation takes place at a distance of ·115 mm. behind the pharynx. This, however, is not a bifurcation in the usual sense of the term, when the

diverticula separate from each other at a somewhat wide angle ; it is rather a division of the œsophagus into two by a thin septum. The two parts run side by side and their lumen is still lined with "cuticle." Intestinal epithelium does not appear till a further distance of ·05 mm., and immediately thereafter the diverticula proper arise. This structural peculiarity of the œsophagus has not been noted by any previous author and is not indicated in Braun's figures. It is probable, however, that the small transverse parts in Br. palliatum and the other two species, joining the undivided œsophagus to the main diverticula correspond with the parts which I have described above, and that they are lined by cuticle and therefore functionally part of the œsophagus. Around the anterior end of the œsophagus are several groups of rather large cells, which probably correspond to the salivary glands of Br. palliatum as described by Looss.

The diverticula occupy the lateral fields midway between dorsal and ventral surfaces and extend to within a short distance of the posterior end of the body, turning in towards the middle line at their termination. In addition to the main diverticula a pair of smaller diverticula, one on each side, pass forwards and reach almost the level of the middle of the oral sucker. These secondary diverticula are distinctive of the genus. The condition of the diverticula does not differ from that in the other species. They pursue a very erratic course, and numerous dilatations of various sizes, never attaining the size of twigs, are found both on their outer and inner sides. The sinuosities are so numerous and irregular that on section the diverticula present the appearance of being traversed by trabeculæ. The condition suggests that the diverticula, originally simple, had grown too long for the body and had become at first regularly sinuate and then crushed up to be accommodated in the limited space.

The structure of the intestinal wall is identical with that described by Looss. The epithelium is well developed and presents numerous villus-like projections. The muscular

coats of the œsophagus are well marked but those of the diverticula are thin.

As already noted the excretory aperture opens on a large pit-like depression at the posterior end of the body; whether this depression is an intrinsic part of the excretory system or not I am at a loss to say. Small cuticular spines penetrate a short distance within it, and the rest of its surface is lined by a thin membrane which appears like cuticle but is much thinner than the body cuticle. It may be either an invagination of the posterior end of the body, or a dilatation of the terminal part of the excretory duct, or both combined. A similar condition has not been observed in the other species of the genus, and as it is only visible on section Braun was not able to observe it. It was present in each of my specimens. Its significance is not apparent.

A narrow tube with muscular walls leads from the aperture to the vesicle. Several muscle-fibres are grouped round the aperture in the form of a sphincter. The vesicle itself is of simple structure. It is lined throughout by a thin, delicate membrane, in which small scattered epithelial cells can be observed. The wall is extremely irregular, being thrown into innumerable little wrinkles and folds. There is a deposition of muscle-fibres, both annular and longitudinal, but they are very fine. The vesicle lies in a mass of very loose connective tissue, and it extends as far forward as the posterior border of the ovary, passing dorsally to the testes, by which it is compressed, but expanding in the spaces between the testes and ovary. The anterior end is flattened and broadened and into it the two lateral tubules enter. These pass forwards and are distributed in the manner which Looss has fully described in Br. palliatum.[1]

The genital aperture is median, close in front of the ventral sucker. It is a narrow transverse slit with sphincter and radiating muscle-fibres. The genital sinus is of small size. The male duct opens into it on the right, the female on the left. The radial fibres of the genital aperture pass into the

[1] Op. cit., p. 405

longitudinal fibres of the cirrus-pouch and vagina. The cirrus-pouch (fig. 7) is a pear-shaped or ovoid structure extending backwards nearly as far as the posterior border of the ventral sucker. It thus reaches further back than in any other species of the genus. At its posterior end it approaches the dorsal surface of the body, and is separated from the ventral sucker by the uterus. Its maximum diameter is ·3 mm. The longitudinal muscle-fibres of its wall have a diameter of ·002–·004 mm., and are separated by spaces of ·001–·004 mm. The annular fibres are much finer, ·0004–·002 mm., with intervening spaces of ·0007–·0015 mm. The vesicula seminalis is of large size and occupies the greater part of the cirrus-pouch. Its length is about ·8 mm., but it displays numerous dilatations and convolutions. Its diameter varies from ·16 mm. to ·28 mm. At its anterior end its wall is slightly invaginated into the pars prostatica, which is a short S-shaped tube with a diameter of ·066 mm. The prostatic cells are comparatively few and are entirely confined to the space around the pars prostatica. The cells are oval, with a long diameter of ·012 mm. and nuclei of ·0035–·004 mm. diameter. Amongst the prostatic cells there are a few larger cells measuring ·019 mm., which do not stain so deeply and have faintly-staining, round nuclei measuring ·0062 mm. At its anterior end the pars prostatica passes into a widely dilated ductus ejaculatorius, which presents a rather unusual condition. In its retracted state, instead of being convoluted or wound upon itself, as is the case in many species, it is crumpled up (concertina-fashion). In sections it presents a grating-like appearance (fig. 7), the lumen being alternately contracted and expanded. The crumpling, however, is not by any means irregular, fairly equal spaces being maintained between the folds.[1] The structure of the wall of the ductus does not differ from that commonly met with, there being an

[1] A somewhat similar condition appears to exist in Distomum alacre Lss., according to Looss's short description of that species ('Centralbl. f. Bakter.,' Abth. 1, vol. xxix, p. 401). In the genera Fellodistomum and Steringophorus an analogous condition exists, but in these the ductus is very short.

inner layer of well-marked annular muscle-fibres and an outer layer of less distinct longitudinal fibres. The lumen is lined by a rather thick cuticularised epithelium. In addition, however, to the two intrinsic muscle layers there are numerous other stout muscle-fibres passing from the ductus to the wall of the cirrus-pouch. These run more or less obliquely, but on eversion of the ductus they are drawn nearly parallel to it. To explain this peculiar condition of the ductus it seems necessary to consider that these extrinsic muscle-fibres exert the most important action in retracting the ductus from its everted position and that on account of their direction they cause it to fold up instead of winding on itself. What action the intrinsic longitudinal fibres take or why the eventual result should be so different from that most frequently observed are questions not easy to determine. No mention is made of such a condition by Looss in the case Br. palliatum. His figure (Pl. XXIII, fig. 8) represents the ductus as a slightly tortuous tube of uniform calibre, widening somewhat suddenly as it passes backwards and surrounded by a closely packed mass of gland-cells (Anhangsdrüsen). The condition is therefore totally different from that in Br. oblongum, and it is a curious fact that two so closely related species should present such an important feature of difference. Cells which stain deeply (gland-cells or myoblasts) are certainly present around the ductus, but they are comparatively few in number and scattered in the midst of looser tissue.

That the terminal part of the ductus functions as an exsertile cirrus there can be no doubt, for in one of my specimens I found it extended about ·06 mm. beyond the genital aperture (i. e. about ·2 mm. from the male aperture). In that case the anterior folds of the ductus were straightened out, but the posterior folds remained, so that while the anterior part became a tube of uniform calibre, the posterior part remained in the condition above described.

The histological structure of the pars prostatica and vesicula seminalis does not differ from that in Br. palliatum.

The lining epithelium appears to be of somewhat lower type, and the muscle-layers are rather finer.

From the posterior end of the vesicula seminalis a single vas deferens, ·023 mm. in diameter, passes backwards to the level of the middle of the ovary, where it divides into the paired vasa. These remain close together for a short distance and then separate to enclose the ootype. They join the testes on their dorsal surface.

The testes are median, close together, and directly behind each other. They occupy almost completely the middle third of the body, the posterior testis being exactly one third from the posterior end of the body, and the anterior testis a slightly greater distance from the anterior end. Each has a rather peculiar shape, differing from that of the other. The anterior testis is twice as broad as it is long, and its thickness equals its length. It is therefore much compressed in the long axis of the body; not only so, but there is a distinct hollowing out both on the anterior and posterior surfaces, which is obvious only on longitudinal section. It consists of four lobes, two large lateral with small anterior and posterior lobes. The posterior testis is much more symmetrical, being composed of four nearly equal lobes—an anterior, a posterior, and two lateral. The anterior lobe is slightly indented on its ventral aspect, and the posterior shows one or two irregularities, but the lateral lobes are almost uniformly rounded. The lobing is quite deep, and the central part of the testis is about equal in size to each of the lobes. This testis is almost iso-diametric, and its maximum thickness is about half its diameter. The thickness diminishes from the centre to the periphery. This symmetrical shape might be regarded as the normal condition of the testes, and the shape of the anterior testis as the result of deformity. In Braun's figure (fig. 3) the testes are shown as irregularly four-lobed bodies. The particularly long posterior lobe of the hinder testis, to which Braun draws attention, is evidently not a constant feature. In Br. palliatum the testes are lobed, but the lobes are smaller, more numerous, and do not appear

to have any constant direction. In Br. delphini and Br. rochebruni they are regularly ovoid. In a specimen of 5·5 mm. length the sizes of the testes are: Anterior, length ·54 mm., breadth 1·20 mm., thickness ·55 mm.; posterior, length ·93 mm., breadth 1·02 mm., thickness ·52 mm. Thus the diameter of the posterior testis is two elevenths of the body length.

The ovary is median or very slightly to the right side, directly in front of the anterior testis and close to the ventral surface of the body. It is separated from the ventral sucker by a very short space. Braun is not quite correct in saying that the ovary is globular in shape, for I find it constantly slightly elongated transversely. The mean of three measurements gives the length ·30 mm., breadth ·37 mm., thickness ·28 mm. The ovarian ova are largest towards the anterior-dorsal surface, and measure ·0155 × ·0087 mm. They are fusiform in shape, with large, round nuclei, measuring ·0077 mm. Looss has figured and described the corresponding cells of Br. palliatum, and it is evident that our observations agree fairly closely, except that I find the cells constantly rather more elongated. It is true, however, as Looss remarks, that these cells undergo various changes in shape.

The shell-gland complex (fig. 6) in this species differs in more than one respect from that of Br. palliatum, as described by Looss, and particularly in the greatly reduced size of the receptaculum seminis and the presence of a distinct yolk-reservoir. The oviduct (diameter ·029 mm.) arises from the dorsal surface of the ovary. Not far from its origin it describes a complete circle upon itself and then passes on in a straight course. About midway between the ovary and the dorsal surface of the body it dilates slightly and then turns at right angles towards the left. At this point there is a small sacculation, on the right side, no wider than the oviduct itself, and not differentiated from it by any marked constriction. This is all that remains of the receptaculum seminis, and in all probability it no longer functions as such, for it never contains sperms and its lumen is almost entirely

filled up with the hair-like processes of the epithelial cells. Moreover, its function seems to have been undertaken by the initial part of the uterus, which in every specimen is packed full of sperms (receptaculum seminis uterinum). Almost immediately beyond the above-described turning of the oviduct Laurer's canal arises. It has a peculiar and almost constant course. It passes first towards the dorsal surface, bending slightly to the left, but after traversing half the distance it turns suddenly at right angles and runs posteriorly parallel to the dorsal surface for a considerable distance, describing at the same time almost a complete semi-circle with its convexity towards the right. It then again turns abruptly at a right angle and passes in a more or less direct course towards the dorsal surface, where it opens almost in the middle line on the level of the anterior border of the anterior testis or a little further forwards. Its diameter is about ·023 mm.

From the origin of Laurer's canal the oviduct proceeds on its way towards the ootype, running almost parallel to the surface of the ovary. Just before entering the ootype it receives the common yolk-duct, which passes forwards in a rather sinuous course from a small reservoir lying a little in front of the anterior testis and almost midway between the ovary and the dorsal surface. The ootype, which is situated dorsal to the left end of the ovary, bends forwards and dorsally to pass into the uterus. The ootype is wider (diameter ·033 mm.) than the oviduct and the uterus is still wider. The shell-gland is of large size. It does not invest the ootype closely, but its cells are diffusely scattered in the surrounding parts and communicate with the ootype by means of long ducts. They are most numerous around the oviduct and common yolk-duct. The histological structure of the shell-gland complex conforms to the usual type. The whole course of the oviduct is lined by a thick ciliated epithelium. The cilia are fairly long and are directed away from the ovary. The receptaculum seminis is also lined by this ciliated epithelium, the cilia of which are so numerous that they

almost obliterate the cavity of the receptaculum. At irregular intervals in the epithelium of the oviduct there are single large cells, evidently the same as those observed by Looss in Br. palliatum.[1] For a very short distance Laurer's canal is also lined by ciliated epithelium, the cilia of which are directed towards the ovary, i. e. in a direction opposite to that of the cilia in the oviduct. It is evident that this arrangement has some relation to the prevention of the escape of ova or sperms through Laurer's canal. An analogous condition has been observed by Looss in Distomum unicum Lss.[2] The remainder of Laurer's canal is lined by a cuticularised epithelium. The ootype is lined by a regular non-ciliated epithelium. The cells of the shell-gland do not have the dense arrangement represented by Looss in Br. palliatum.[3] They are fairly large cells, measuring ·020 by ·012 mm., and nuclei ·005 mm.

The yolk-glands are richly developed, extending from the level of the pharynx to the posterior end of the body. They are mainly lateral, but their situation is not so much marginal as ventral and dorsal to the intestinal diverticula. Behind the testis they unite in the middle line, also to a slight extent in front of the genital aperture. The follicles are not very large, about ·07–·08 mm. diameter. The component cells are not well differentiated, owing to their containing a large number of bright yellow refracting granules, which are about ·003 mm. in size. These granules are very difficult to stain, remaining untouched long after the other tissues are deeply stained, but eventually they do take on the stain. I found that they did so more readily with saffranin and tolnidine-blue than with hæmalum and eosin. The small (·004 mm.) round nuclei of these cells stain readily enough. I was quite unable to determine any differentiation between central cell and peripheral cells as in Stephanophiala

[1] Op. cit., pl. xxiii, fig. 10.

[2] "Recherches sur la faune parasitaire de l'Egypte"; in 'Mém. Inst. Egypt,' iii (1896), p. 49.

[3] 'Zeitsch. f. wissen Zool.,' xli, pl. xxiii, fig. 13.

laureata. The transverse ducts run along the anterior border of the anterior testis to unite in the small median reservoir. This contains a small number of yolk-cells in which the nuclei are still present. The common yolk-duct passes forward to join the oviduct as already described.

It appears to be quite erroneous to speak of the secretion of the yolk-glands, as so many observers have done, for as I have shown both in the case of Stephanophiala laureata and the present species, the yolk substance is the result, not of a process of secretion, but of a process of proliferation of formative cells in a manner somewhat analogous to the production of ovarian ova or spermatozoa. The yolk-glands must therefore not be regarded in the same category as the shell-gland and prostate-gland, which produce a true secretion. They are glands only in the same sense as the ovary and testes are glands.

As in Br. palliatum, the uterus is confined to a very limited space between the ovary and the level of the genital aperture and between the intestinal diverticula on either side. It thus lies dorsal to the ventral sucker and occupies the entire thickness of the body. Its course is impossible to determine, owing to the greatly convoluted condition. The initial part, from the ootype, is lined with a highly ciliated membrane, but the cilia disappear after a short distance. The uterus then becomes distended with ova, which are surrounded by a countless number of sperms. This condition persists for about a third of the total length of the uterus, and it is evident that we have here to deal with a true receptaculum seminis uterinum, which is met with in several other species and which performs the function of the vestigial receptaculum seminis proper. The condition here is evidently much removed from that in Br. palliatum, in which, according to Looss, the receptaculum seminis is full of sperms, and performing its true function, while no mention is made of a receptaculum seminis uterinum.

The uterus terminates near the dorsal surface of the body, and the vagina passes almost in a straight line, dorso-

ventrally, towards the genital sinus. It has a length of ·45 mm., and a diameter of ·04–·09 mm., becoming narrow as it approaches the genital sinus. Its section is not circular, but triangular, and this is constant in every case, being apparently in correlation with the triangular shape of the ova. Its wall is thick (·012 mm.) and muscular, comprising the usual two layers, and it is lined by a thick cuticular membrane.

The ova are fairly numerous and measure ·084 by ·0436 mm. The shell is light yellow and about ·0035 mm. thick. The shape is characteristic. In longitudinal section they are somewhat oval, but truncate at the anterior end and with a pointed knob, due to a thickening of the shell, at the posterior end. The operculum is very flat. In transverse section, however, they are triangular, the triangle being equilateral. This peculiar shape of the ova was first noted, I believe, by Odhner[1] in the case of Orthosplanchnus arcticus Odh., O. fraterculus Odh., Lecithodesmus goliath (v. Ben.), and Brachycladium oblongum (Brn.). In his diagnosis[2] of the sub-family Brachycladiinæ Odh. he regards it as a distinctive feature differentiating the sub-family, amongst other things, from the Fasciolinæ. He thus considers it to be of universal occurrence in the sub-family, and in particular in the genus Brachycladium Lss. He refers[3] to Poirier's[4] figures of the ova of Br. rochebruni and Br. delphini as indicating that the ova of the species probably display the same shape. I fail to see any evidence of this in Poirier's figures, and he himself certainly makes no reference to the triangular shape of the ova in transverse section.[5] Odhner conveniently ignores Looss's statement[6] that

[1] "Die Trematoden des Arktischen Gebietes" in 'Fauna Arctica,' iv, p. 343.

[2] Ibid., p. 347.

[3] Ibid., p. 346.

[4] "Trematodes nouveaux ou peu connus," in 'Bull. Soc. Philomatique, Paris,' sér. 7, vol. x, pl. iv, figs. 3 and 5.

[5] It is quite possible that Odhner only means to imply that the ova in Poirier's two species resemble those of the other Brachycladiinæ in being thick shelled, with flat operculum and pointed posterior end, but his statement in the sub-family diagnosis renders this doubtful.

[6] 'Zeitsch. f. Wissen. Zool.,' xli, p. 419.

the ova in Br. palliatum "haben fast die Gestalt eines Rotationsellipsoides." His hypothesis, therefore, although highly probable, requires confirmation, and Looss's observation must first be proved erroneous.

From the foregoing description it will be apparent that Brachycladium oblongum (Brn.) and Br. palliatum (Lss.) cannot be confused, for the two species differ not only in their coarser anatomy, as Braun has already demonstrated, but also in many of the finer details. It will also be admitted that Br. oblongum does not conform strictly to the type of Br. palliatum, but differs from it in such important features as the structure of the ductus ejaculatorius, the reduced condition of the receptaculum seminis, with the presence of a receptaculum seminis uterinum, and possibly most important of all, the shape of the ova. How far any or all of these divergences are due to an error of observation on Looss's part, particularly as regards the ova, it is impossible to say, but assuming them to be correct there can be little doubt that the two species cannot be included in the same genus. Not only so but the condition of the ova would render Br. palliatum Lss. an atypical member of the Brachycladiinæ according to Odhner's diagnosis. On the other hand, Br. oblongum conforms to the sub-family definition, but is an aberrant member of the genus Brachycladium Lss. (type Br. palliatum Lss.). At present it seems best to await fuller knowledge of Poirier's species before pronouncing judgment on the matter.

Sub-family Allocreadiinæ (Lss. 1899).

Genus Lebouria n. g.

Lebouria idonea n. sp., Pl. 9, figs. 9–12.

This form occurred very regularly and always in large numbers throughout the intestine of Anarrhichas lupus. It also occurred less frequently in the stomach. It is easily

seen in the midst of the intestinal contents on account of its distinctly yellow colour.

It is of medium size, 1·5–2·5 mm. long, with a maximum breadth of ·7–1·0 mm. Thickness ·2 mm, fairly uniform except at the ventral sucker, where it reaches ·3 mm. Its breadth is therefore nearly half its length, so that it is broader than most other Allocreadiinæ. The shape is oval, slightly attenuated anteriorly, considerably flattened dorso-ventrally. One example showed a curious deformity. In the posterior half of the body on the level of the testis there was a large indentation on the right side, an appearance as if a part had been bitten out. The specimen was uninjured, and although it was alive and moving actively the deformity still remained. It may be regarded as a pathological curiosity.

The smallest mature specimen obtained measured 1·58 mm. The largest immature specimen had the same length, and many were found without ova just about this size or a trifle smaller, so that this probably represents the size at which ova begin to appear, and may be taken as the minimum length of adult specimens. The smallest immature example measured 1·23 mm.

The cuticle is about ·004 mm. thick and entirely without spines. True unicellular cutaneous glands, of the same kind as already described in Stephanophiala laureata, are present in the anterior part of the body, chiefly laterally. They are large, oval cells with distinct nuclei, and with their long axis in the length of the body, but they differ in appearance from the corresponding cells in St. laureata. They present a very distinct outline with pale, scanty, granular contents. This may be due to a difference in the condition of the cells or possibly to a slight difference in staining.

The subcutaneous muscular system is as usual. The circular fibres measure ·0005 mm. and are separated by spaces of ·004 mm. The longitudinal fibres measure ·0007 and are separated by ·0135 mm. The diagonal fibres measure ·001 mm. with spaces of ·045–·055 mm. The muscles throughout the rest of the body are well developed, especially

in the neighbourhood of the ventral sucker. The myoblasts of the subcutaneous muscles are numerous, and arranged in groups. Their nuclei measure ·004–·005 mm.

The oral sucker is subterminal and nearly round, measuring ·17–·28 mm. The ventral sucker is situated very nearly in the middle of the body and is transversely oval. Its long axis measures ·41–·58 mm., its short axis ·31–·48 mm. It is thus about twice the size of the oral sucker, and the transverse diameters of the suckers are respectively about one tenth and two ninths of the body-length. The internal structure of the suckers offers nothing peculiar.

The pre-pharynx is distinct and rather wide. The pharynx is of comparatively large size, measuring ·15–·21 mm. in diameter. It is nearly globular, but the breadth is slightly greater than the length. It is proportionately much larger than it is in any other member of the Allocreadiinæ. The œsophagus is about as long as, or a little shorter or longer than, the pharynx (·1–·18 mm.). In section it is transversely oval. The intestinal bifurcation occurs almost midway between the suckers. The diverticula are fairly wide (·04–·07 mm. in a large specimen). They pass round the sides of the ventral sucker and, taking up a dorsal position, extend nearly to the posterior end of the body. The œsophagus is sharply differentiated from the diverticula, not only by the change in the nature of the lining, but also by a well-marked constriction (fig. 10). The bifurcation is of the nature of a dilated sac formed by the fusion of the initial parts of the diverticula. In appearance it rather simulates a small ventricle. The pharynx and œsophagus are lined with a cuticular membrane; that of the former is probably true cuticle, that of the latter is transformed epithelium. In any case the two are not identical, for the pharyngeal lining is thicker and stains more deeply than the œsophageal. The bifurcation and diverticula are lined throughout by a well-developed epithelium, the nuclei of which are round and measure ·0052 mm. Numerous hair-like processes are given off from the cells. The musculature of the alimentary canal

is well developed. The fibres of the œsophagus are stouter and more closely set than those of the diverticula. They have a diameter of about ·0015 mm., and are separated by about the same distance or slightly more in the case of the longitudinal fibres. Those of the diverticula measure ·0004 mm. with spaces of ·0035 mm. in the case of the annular fibres, and ·0075 mm. in the case of the longitudinal fibres. These figures of course are only approximate, for there is great variation with the state of contraction. A moderate number of circum-œsophageal cells (myoblasts) are present.

The excretory system is of simple type. There is a small undivided vesicle not extending further forward than the anterior testis and opening by a pore at the posterior end of the body. From the vesicle two narrow, transversely oval, collecting tubes are given off. They pass outwards to lie close to the outer side of the intestinal diverticula. Their course thereafter was not followed.

The testes are two transversely-oval bodies of rather irregular outline lying midway between the ventral sucker and the posterior end of the body. They are very close together, practically contiguous, and very often somewhat obliquely set, one behind the other. The anterior testis is displaced to the left side, while the posterior is nearly median or a little to the right. In many specimens they were found directly tandem, but no other difference could be found in those specimens, so they are probably only a variety. The testes are very nearly equal in size, the posterior being, if anything, a little larger. The long diameter measures ·31–·37 mm., the short diameter ·19–·22 mm. The vasa deferentia arise from their anterior surface and pass forwards ventral to the shell-gland complex as two almost straight lines towards the vesicula seminalis.

The cirrus-pouch (fig. 11) is of no great size, but it appears shorter than it actually is, owing to the backward displacement of the ventral sucker. It extends only a short distance beyond the anterior border of the sucker. Its total length is about ·4 mm. The narrow anterior part, which has a terminal

diameter of about ·03 mm., usually runs straight back from the genital aperture, while the thicker part is bent on this either to the right or left. The diameter of the latter reaches a maximum of ·09 mm. Its wall consists of the usual double layer of muscle-fibres, which have a diameter of about ·0009 mm. and are closely set. The vesicula seminalis is remarkable for the extent to which it is convoluted (fig. 11), exceeding that of Podocotyle atomon (Rud.) in this respect. It appears, however, to have a fairly definite configuration. From the end of the cirrus-pouch it passes forwards in a curve towards the right. It then turns completely on itself and bends back in an S-shaped course nearly to the posterior end of the pouch, where it again turns and runs forward almost parallel to the first part. It then passes into the ductus ejaculatorius, which almost immediately bends backward, describes a turn, passes forwards again, only to describe another complete turn, after which it runs forwards in a sinuous manner, but without further convolutions. The diameter of the vesicula seminalis is ·04 mm.; that of the ductus is about ·015 mm.

As in Podocotyle atomon (Rud.) no well-differentiated pars prostatica occurs on the ductus. Around the initial part of the ductus, however, there is a considerable number of large cells which occupy the usual position of the prostatic cells. They differ from the corresponding cells in Stephanophiala laureata, Brachycladium oblongum and other species which I have examined. The cell body appears to be very tenuous and almost invisible, but the nucleus and nucleolus stain very brightly. The nucleus is large and round, measuring ·0068 mm., the nucleolus ·0018 mm. They certainly do not lend the impression of being gland-cells, but from their position they can hardly be otherwise. They are quite distinct from the "Begleitzellen" or myoblasts which are present in large numbers around the anterior two thirds of the ductus. The latter are much smaller cells, staining deeply and resembling the peri-vaginal cells.

The genital aperture is situated midway between the

suckers, just over the intestinal bifurcation. In most specimens it is approximately median, but in many it is displaced a little to the left side, and in a few a little to the right. The normal position may therefore be regarded as median, but with variations, and this probably indicates one of the initial stages of the transformation to a distinctly lateral position as in Podocotyle. The only other members of the ALLOCREADIINÆ, as at present recognised, which have a lateral genital aperture, are A. tumidulum (Rud.) and A. angusticolle (Hausmann), in the former of which the aperture is well to the left, in the latter only slightly. In all the other species it is median, and it is surprising that more forms have not been described showing intermediate stages of this displacement, for it is evident that it can only have occurred by a gradual series of changes. It would be interesting to discover the reason of the transposition and why it is to the left.

A small genital sinus is present, into which the male duct opens on the right, the female on the left.

The ovary is situated immediately in front and to the right side of the anterior testis, with which it is contiguous. It also lies close beside the intestinal diverticulum, and is separated from the ventral sucker by a distance equal to the diameter of the ovary. It is a round, almost globular body, with entire margin and measures ·16–·17 mm. in diameter. The ovarian cells are largest anteriorly, being abont ·01 mm. in size. The oviduct arises from the anterior dorsal surface of the ovary, and passes in a curved course towards the receptaculum seminis. This is a large oval sac, measuring ·1–·16 mm., attached to the oviduct without the intervention of a pedicle. Laurer's canal arises directly from the receptaculum and runs almost straight in towards the middle line of the body. The exact position of its opening could not be ascertained. The receptaculum lies dorsal to the ovary, but its position is variable, being sometimes in front of the ovary, sometimes behind it. In fig. 12 it is shown in the latter position. From the receptaculum the oviduct passes across the ovary to the shell-gland, before entering which it is

joined by the common yolk-duct. The shell-gland lies close to the left side of the ovary and receptaculum. It is a small, compact structure with cells measuring ·015 mm. and nuclei ·0058 mm. The cells have a distinct staining reaction, taking on a uniform dull red or reddish-purple with hæmalum-eosin.

The small yolk-reservoir lies dorsally in the middle line of the body just in front of the anterior testis. The yolk-glands are lateral, extending from the pharynx to the posterior end of the body, where they unite behind the testes. Anteriorly a few follicles find their way across the middle line under the dorsal surface, but none ventrally. Posteriorly the follicles lie under both the dorsal and ventral surfaces and surround the intestinal diverticula. They are of moderate size, comprising twelve to twenty cells, which measure about ·023 mm. in diameter, and have large (·006 mm.), round, central nuclei.

The uterus is limited in extent, being confined between the ovary and the posterior border of the ventral sucker, but also filling up the space between the sucker and the left intestinal diverticulum. The vagina is shorter than the cirrus-pouch, lying to the left of it and slightly dorsal. Its diameter diminishes from ·035 mm. to ·023 mm. It has the usual muscular structure with numerous accompanying myoblasts.

The ova are not numerous (about sixty). They are light yellow, with a very thin shell. Their shape is broadly oval, but at the anopercular pole there is a small excrescence of the shell forming a small knob-like projection.[1] This is of variable size and is sometimes absent. It might be regarded as indicating an initial stage towards the filamented condition of the ova in Helicometra. They measure ·0715–·0746 mm. in length by ·039–·0435 mm. in breadth. Average ·073 by ·041 mm.

From Anarrhichas lupus six species of Distomids have at one time or another been recorded. The first of these are two species mentioned by Rathke[2] and named by Rudolphi[3] Distomum incisum and D. anarrhichæ lupi, found re-

[1] For directing my attention to this I am obliged to Miss Lebour.

[2] 'Dansk. Selsk-Skrift,' v (1), (1799), p. 70, pl. 2, figs. 3, a, b.

[3] 'Entoz. Hist. Nat.,' ii (1), (1809), pp. 361, 435.

spectively in the intestine and the stomach. The description of both is extremely scanty and hardly admits of positive identification. D. incisum, it is true, was regarded as identical with D. fellis Olsson by Stossich, but this is denied by Jacoby.[1] It is almost certain that neither species is identical with Lebouria idonea. Distomum atomum Rud. is noted by von Linstow[2] under Anarrhichas lupus, but in the reference[3] it is only recorded from Platessa flesus. The peculiar condition of the ova which von Linstow describes distinguishes his specimens from Podocotyle atomon (Rud.), and renders it not at all improbable that they were really specimens of Lebouria idonea. The first mention of this actual species is by Miss Lebour,[4] who has kindly allowed me to describe it in consideration of a previous communication of its discovery which I had made. It is not the only species which occurs frequently in the intestine of Anarrhichas lupus, for in invariable association with it, but usually in the lower parts of the intestine, I have met the much smaller form Zoogonus rubellus (Olsson). This is the first record of the latter species from the cat-fish, and also the first time it has been met with in British waters, yet it is a constant parasite of the cat-fish in this locality.

It remains to differentiate Lebouria idonea from already recognised members of the sub-family Allocreadiinæ. From Podocotyle (Duj.) it is easily distinguished by the median position of the genital aperture; from Helicometra Odhner by the non-filamented condition of the ova, and from Allocreadium Lss. sens. str., by the oblique position of the testes, the backward situation of the ventral sucker, and the absence of distinct pars prostatica. Amongst the unclassified forms it appears to bear most resemblance to Distomum tumidulum Rud.,[5] but that species is more elongated, has a

[1] 'Arch. f. Naturg.,' lxvi, p. 13.

[2] 'Compend. d. Helminth. Nachtrag.,' p. 82.

[3] 'Arch. f. Naturg.,' xliv, p. 225.

[4] 'Northumberland Sea Fisheries Report for 1907,' p. 16.

[5] Odhner, "Revision einiger Arten der Distomumgattung Allocreadium Lss.," in 'Zool. Jahrb. Syst.,' xiv, pp. 503–505.

distinctly lateral genital aperture,[1] smaller ova, and round testes. Were it not for the lateral genital aperture it might readily enough be included in the genus Lebouria, and it is certainly more nearly related to this genus than it is to Podocotyle. This affinity may be indicated by re-naming the species (Lebouria) tumidula Rud. From the other ALLOCREADIINÆ, Lebouria idonea is much more easily distinguished.

In proposing this species as the type of a new genus I have been influenced by the fact that it is impossible to include it under the genus Allocreadium Lss., and therefore its description as an Allocreadium sp. would have been erroneous. Moreover, it appears to be the representative of a group with features quite as well defined as those of Helicometra and Podocotyle, and further, it is not an isolated species, for in an American form described by Linton[2] from Bairdiella chrysura we have what must be regarded as an additional number of the genus. Linton's work is, unfortunately for our present purpose, more of a bionomic than morphological character, so that his treatment of the species is not so exact as we might have desired. His figures, however, give a fairly good idea of the form, and its close resemblance to Lebouria idonea is not difficult to make out. We note the expanded shape of the body, the backward position of the ventral sucker with the intestinal bifurcation far in front of it, the oblique, or sometimes median, position of the testes, the round ovary, extensive yolk-glands, limited uterus, short cirrus pouch, and median genital aperture. With regard to the position of the genital aperture it is shown in fig. 168 midway between the ventral sucker and the intestinal bifurcation, but from the forward position of the ova it may possibly be found to be somewhat

[1] I have since found in Labrus bergylta a Distomid which I am inclined to identify as Distomum tumidulum, and in it the genital aperature is median or very slightly displaced.

[2] 'Bull. Bureau U.S. Fisheries,' xxiv (1904), p. 389, pl. xxiii, figs. 168–170.

nearer the bifurcation. Linton was somewhat doubtful of the identity of this species and hesitated to assign to it a specific name. I therefore propose for it the name Lebouria obducta n. sp., and add the following short description.

Length about ·8 mm.; breadth half the length; oral sucker ·12 mm.; ventral sucker oval, a little in front of the middle of the body, diameter ·17 mm. (this is probably the short diameter, for in Linton's figures the transverse diameter is always at least twice that of the oral sucker). Pharynx, length ·06 mm.; œsophagus short; genital aperture a little behind intestinal bifurcation. Testes much larger than those of Lebouria idonea, irregularly shaped, in posterior third of body. Cirrus-pouch short, extending a little beyond the anterior border of the ventral sucker. Ovary transversely oval, on a level with anterior testis or a little in front, on right side. Yolk-glands only reaching intestinal bifurcation, not uniting in front but filling up space behind testes. Ova few (five to twenty) measuring ·063 by ·035 mm.

From a comparison of these two species the genus Lebouria may be defined as follows:

Small Allocreadiinæ with broad, flat, oval body. Ventral sucker oval, larger than oral sucker, situated about the middle of the body or a little in front of it. Œsophagus short, intestinal bifurcation midway between suckers. Excretory vesicle simple, short. Genital aperture median or slightly displaced, near the intestinal bifurcation. Testes of irregular shape, oblique or tandem, in the middle of the post-acetabular region. Cirrus-pouch short, not reaching the middle of the ventral sucker, containing a convoluted vesicula seminalis and ductus ejaculatorius, but lacking a well-differentiated pars prostatica, although prostatic cells are present. Ovary rounded, on the right side, on a level with anterior testis or immediately in front of it. Receptaculum seminis and Laurer's canal present. Yolk-glands extending in front of ventral sucker. Uterus short; ova few, thin-shelled, with small protuberance at the anopercular pole, measuring about ·07 by ·04 mm.

Habitat.—Stomach and intestine of marine fishes.

Type. — Lebouria idonea n. sp.; including also L. obducta n. sp.

Mention may be made here of another species which bears some resemblance to Lebouria idonea, namely, Distomum alacre Lss.[1] from Labrus maculatus and other Labridæ. At first sight only comparatively unimportant differences are apparent between the two, such as the slightly lateral position of the genital aperture, the somewhat elongated testes and the rather larger ova. The structure of the terminal part of the male genital duct, however, is different from that not only in Lebouria but also in other ALLOCREADIINÆ, and for that reason, apparently, Looss has hesitated in assigning to this species a systematic position.[2]

Genus Podocotyle (Duj.) Odhn., 1904.

= Sinistroporus Stafford, 1904.

Podocotyle atomon (Rud.) Pl. 10, fig 28.

= Distomum vitellosum Linton. Johnstone, 'Report Lancashire Sea Fisheries,' for 1906, xxi (1907), pp 182–185, fig. 15.

For the opportunity of examining these specimens I am indebted to my friend Mr. Johnstone, who kindly put them at my disposal. Their resemblance to Distomum vitellosum Linton is not borne out on close examination, and they have proved to be in reality a species of Podocotyle, most probably P. atomon (R.). At first sight I was inclined to regard them as distinct from the latter species. The unusually cylindrical shape of the body, the excessive

[1] 'Centralbl. fur Bakter.,' 1st Abth., xxix, pp. 401–402, fig. 2.

[2] In a paper by Stossich (in 'Boll. Soc. Adriat.,' xxii, p. 211–217), which has not yet found its way into the London libraries and which I have therefore not had an opportunity of seeing, Distomum alacre Lss. is included in the genus Allocreadium (not sens. strict). If this species be really a member of the ALLOCREADIINÆ it must occupy a place very near the genus Lebouria.

prominence of the ventral sucker and the conspicuousness of the yolk-ducts were features unfamiliar to me in my previous experience of the species. As a matter of fact, however, they are due to the method (in fresh water) which Johnstone employed in killing his specimens. I have since found Podocotyle atomon in various species of fish, and tried the experiment of killing some in fresh water, in which they assumed the same shape and appearance as Johnstone's specimens.

One of the most striking features of Johnstone's specimens was the distinctness not only of the yolk-ducts but also of the yolk-glands themselves. On that account their disposition could be easily observed, and this is shown very well in Johnstone's figure. One point to which he makes no reference is the occurrence, in about every third specimen, of an asymmetrical group of follicles in front of the ventral sucker on the right side. This had not the linear arrangement of the other follicles, but was more dendritic, and from it a separate duct passed down to join the longitudinal duct. This asymmetrical group was never observed on the left side. I have since collected a number of specimens showing the same characteristic but differing in no other respect from Podocotyle atomon. It seems to indicate what might be regarded as a distinct variety, and for this I propose the provisional name P. atomon var. dispar.

During a recent visit to the Firth of Clyde, I have obtained Podocotyle atomon from numerous species of fish, Gadus virens, G. pollachius, Pleuronectes flesus, Pl. platessa, Cottus scorpius, C. bubalis and Centronotus gunnellus, and have been struck with the remarkable diversity of form which it presents. It displays variation in the extent of the yolk-glands, the length of the cirrus-pouch, the shape and situation of the testes, and, in particular, the size of the ova. I have to add Gastræa spinachia (fifteen-spined stickleback) as an additional host on the east coast, and in the specimens from this host the ova were exceptionally large, reaching a length of nearly ·1 mm. This Trematode, if all the specimens be really identical, is very

widely distributed, it having now been recorded from thirteen different hosts in this country.

On the classification of the Allocreadiinæ.

We are now in a position to recognise, at least, four well-defined groups of the Allocreadiinæ, namely, the genera Allocreadium Lss., sens strict., Helicometra Odhn., Podocotyle (Duj.) Odhn. and Lebouria Mihi. The types of other groups have been indicated by Odhner,[1] and he has also constructed a key for the diagnosis of several species.[2] In all probability the ultimate division of the sub-family will proceed along the lines he has laid down, with certain modifications. The imperfect knowledge which we as yet possess of the internal structure of many of these forms renders premature any attempt at a complete classification of the sub-family, and we must be content for the present with speculations. On the other hand, it is advisable in the interests of systematic work, that as many forms as are sufficiently well known should be assigned their true generic place, and on that account I venture to propose, as the types of two new genera, two species which have already been considered by Odhner as probable generic types, and of which I have personal knowledge,[3] namely, Distomum labracis Dujardin and Dist. genu Rud. Both species have been re-described by Odhner,[4] and the first also by Johnstone.[5] I propose Dist. labracis Duj. as the type of the new genus Cainocreadium with the following provisional definition:

Large Allocreadiinæ with extended, flattened body.

[1] "Die Trematoden des arktischen Gebietes"; in 'Fauna Arctica,' iv, p. 327.

[2] "Revision einig. Arten der Gattung Allocreadiinæ," in 'Zool. Jahrb.,' syst. xiv, p. 516.

[3] Thanks in the first instance to my friend Mr. Johnstone, who sent me his specimens of Allocreadium labracis Duj.

[4] 'Zool. Jahrb.,' syst. xiv, pp. 496–499 and 514–515, pl. xxxiii, figs. 3 and 11.

[5] 'Trans. Biological Soc.,' Liverpool, xxii (1908), pp. 44–53, pl. iii.

Ventral sucker near the middle of the body, globular or slightly oval and not projecting much. Œsophagus short, bifurcation far in front of ventral sucker. Excretory vesicle simple, short. Genital aperture median, not far behind intestinal bifurcation. Cirrus-pouch long and slender, not extending beyond ventral sucker. Vesicula seminalis convoluted, ductus ejaculatorius long; true pars prostatica absent, but prostatic cells present. Ovary on right side, immediately in front of testes, distinctly trilobate. Receptaculum seminis large, giving off Laurer's canal directly. Yolk-glands extensive, filling up considerable part of neck. Yolk-follicles arranged peripherally. Ova without filaments, very variable in size, ·07–·10 mm. by ·04–·06 mm.

For Dist. genu Rud. I propose the new generic name Peracreadium, with the following definition:

Small to medium sized Allocreadiinæ, with elongated ovate, slightly flattened body. Ventral sucker not very prominent, situated about the end of the anterior third of the body. Œsophagus short, bifurcation midway between suckers. Excretory vesicle simple. Genital aperture median, at intestinal bifurcation. Cirrus-pouch very long and slender, extending as far back as the level of the ovary (= about one third of the body length). Vesicula seminalis convoluted; ductus ejaculatorius long; distinct pars prostatica present. Ovary globular, with entire margin, situated a little to the right side of the middle line, immediately in front of the testes or separated from them by a small part of the uterus. Testes usually transversely oval, with entire margin, situated about the middle of the post-acetabular region. Yolk-glands extensive, occupying considerable part of neck and filling up posterior part of body. Ova without filaments, very variable in size, ·07–·10 mm. by ·03–·06 mm.

Habitat.—Labridæ, so far as known.

Type.—Peracreadium genu (Rud.). Also P. commune (Olss).

Between these two new genera the main differences consist in (1) the position of the ventral sucker; (2) the shape of

A Table showing the Chief Comparative Differences between the Six Genera of Allocreadiinæ.

	Helicometra.	Podocotyle.	Allocreadium.	Lebouria.	Cainocreadium.	Peracreadium.
Size	2–3 mm.	1·5–4·5 mm.	2–5 mm.	1–3 mm.	2–10 mm.	1–3 mm.
Shape	Ovate, flattened	Elongated, sub-cylindrical	Elongated, flattened	Ovate, flattened	Elongated, flattened	Elongated, ovate, not much flattened
Length of neck	$\frac{1}{3}$ or slightly more	$\frac{1}{7}$–$\frac{1}{3}$	$\frac{1}{3}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{3}$
Genital aperture	Median	Lateral	Median	Median	Median	Median
Cirrus-pouch	To centre of ventral sucker	More or less beyond sucker	Not beyond centre of sucker	Not beyond centre of sucker	Not beyond sucker	As far back as ovary
Pars prostatica	Present	Absent	Present	Absent	Absent	Present
Ovary	Multilobate	Trilobate	Round	Round	Trilobate	Round
Testes	Irregular	Round or oval	Rounded	Transverse oval	Rounded	Transverse oval
Yolk-glands	In neck	Not in neck	Not in neck	In neck	Much in neck	Much in neck
Œsophagus	Short to medium	Short	Long	Short	Short	Short
Ova	Filamented	Without filaments	Without filaments	Without filaments	Without filaments	Without filaments
Size of ova	·07–·085 mm. ·02–·03 mm.	·07–·095 mm. ·04–·05 mm.	·09 mm. ·06 mm.	·06–·075 mm. ·035–·045 mm.	·07–·10 mm. ·04–·06 mm.	·07–·10 mm. ·03–·06 mm.
Type	H. pulchella (R.)	P. atomon (R.)	A. isoporum Lss.	L. idonea Nic.	C. labracis (Duj.)	P. genu (R.)
Other species	H. fasciata (R.) H. sinuata (R.) H. mutabilis Stoss.	P. reflexa (Crepl.) P. olssoni Odh.	(A.) transversale Rud.	L. obducta Nic. (L.) tumidula R.		P. commune (Olss.)

the ovary and possibly also of the testes; (3) the length of the cirrus-pouch; and (4) the presence of distinct pars prostatica.

Of the remaining unclassified forms nearly related to the Allocreadiinæ I shall refer here only to those described by Stossich[1] and Linton.[2] Of these Distomum umbrinæ Stossich, as already indicated by Odhner, probably represents a distinct genus type, the characteristics of which are: (1) the rather stout, broad body; (2) the very short (or absent) œsophagus; (3) the long cirrus-pouch reaching the ovary; (4) small round testes; (5) globular ovary (on left?); (6) median genital aperture; (7) yolk-glands confined behind ventral sucker. These form a group of features sufficiently important to exclude the species from any of the already formed genera. Distomum obovatum Molin and D. mormyri Stoss. bear much resemblance to each other and to D. umbrinæ Stoss. They differ from the latter, however, in the flatter body, the apparently lateral position of the genital aperture, the yolk-glands extending into the neck, the ovary on the right side and the transverse oval shape of the testes. These three species are probably more nearly related to Peracreadium than to any other genus. Another species which appears to approach those in some degree is that depicted by Linton in fig. 165 and found in Sphenoides maculatus. It is characterised by a very small ventral sucker, a cirrus-pouch just extending beyond the sucker, transverse testes and yolk-glands confined behind ventral sucker. Distomum scorpænæ Rud. Stoss. (I, p. 158, fig. 20) is an extremely doubtful member of the sub-family. It is characterised by the peculiar shape of the body[3] and of the œsophagus. Otherwise it bears a distinct resemblance to Podocotyle, but the ovary is globular and the cirrus-pouch may prove to be of unique structure. Dist. fasciatum Rud.

[1] "Brani Elmint. Tergest.," in 'Boll. Soc. Adriat.,' ix, No. 1 (1885), pp. 158–161, pl. iv–vi; and No. 2 (1886), pp. 44–49, pl. viii.

[2] "Parasites of Fishes of Beaufort, North Carolina," in 'Bull. Bur. Fisheries, U.S.A.,' xxiv (1904). pp. 321–428, pl. xxii–xxiv, xxviii.

[3] This peculiar shape can, however, often be observed in Podocotyle atomon.

Stoss (I, p. 160, fig. 25) is regarded by Odhner[1] as wrongly identified. The long cirrus-pouch brings this species into relation with Peracreadium. In other respects it also agrees closely with this genus.[2]

Distomum vitellosum Linton (p. 335, figs. 176–178) is a species which shows some affinity to the ALLOCREADIINÆ, but is distinguished by the peculiar structure of the ventral sucker. Linton has described this species from numerous fish, but his descriptions are so conflicting that it is either a very variable species or it is a combination of two or more distinct species. It is undoubtedly a genus type, but its structure is not sufficiently well known for it to be definitely included amongst the ALLOCREADIINÆ.

One other species may here be mentioned, namely, Distomum globiporum Rud. Linton (p. 334, figs. 159, 173, 198) from Leiostomus xanthurus and other fish. This species is quite incorrectly identified. It belongs to the subfamily LEPOCREADIINÆ Odhn., but to which genus it is difficult to say. It seems, however, more nearly related to Lepocreadium than to Lepodora (Lepidapedon), and it is not identical with any of the European forms. The specimens which Linton obtained certainly do not all belong to the same species. Those from Fundulus majalis (p. 356, fig. 159) are small with equal suckers, round testes, and apparently without spines, and with the genital aperture immediately in front of ventral sucker. Those from Orthopristis chrysopterus (p. 378) are twice as large, with smaller ova, ventral sucker half as large again as oral sucker. Genital aperture immediately behind pharynx, and vitellaria extending forward to the middle of the neck. Those from Leiostomus xanthurus (pp. 393–394, figs. 173, 198) are a mixed lot, some with spines, others without. The

[1] "Revision der Gattung Allocreadium," in 'Zool. Jahrb.,' syst. xiv, p. 486.

[2] In Stossich's latest paper (see p. 61, note 2) on these species, Allocreadium characis Stoss., A. mormyri, and A. umbrinæ are dealt with. A new species, A. dubium, is added. Whether he deals with Distomum fasciatum Rud. or not I am unaware.

ventral sucker is distinctly larger than the oral sucker, the genital aperture is immediately in front of the ventral sucker, testes lobed, and ova measure about ·10 by ·05–·06 mm. The specimens which Linton found on August 10th, 17th and 30th (pp. 393–394, figs. 198–199) appear to represent a fairly distinct species, the characters of which may be summed up as follows: Length 3 mm.; breadth 1·25 mm. Oral sucker ·4 mm. in diameter; ventral sucker ·5 mm. Cuticle covered with scale-like spines on dorsal surface and anterior ventral surface. Pharynx ·12 mm. Pre-pharynx and œsophagus each about same length as pharynx. Genital aperture median, immediately in front of ventral sucker. Cirrus-pouch extending back to anterior border of first testis. Testes median, tandem, slightly lobed, situated near the middle of the post-acetabular region. Ovary sub-globular not far behind ventral sucker, separated from testes by the end of the cirrus-pouch, median or slightly to right side. Yolk-glands lateral to outer side of intestinal diverticula, filling space behind testes, not extending in front of ventral sucker. Ova not numerous, measuring ·10–·12 by ·05–·06 mm. To this species the provisional name (Lepocreadium) serospinosum sp. inquir (= Distomum globiporum Rud. Linton, 1904, e.p.) may be given.

Sub-family Fellodistominæ, n. sub-fam.

Genus Fellodistomum (Stafford 1904).

Fellodistomum fellis (Olsson, 1868). Pl. 9, figs. 13, 14.

Distoma fellis Olsson, "Entozoa, iakt. Skand. hafsfisk.," in 'Lunds Univ. Årssk.,' iv (8), pp. 44–46, pl. v., fig. 94, A, B.

Distomum fellis Olsson, Stossich, "I. Distomi dei Pesci," in 'Progr. d. Ginnasio comm. super. Trieste.,' 1886, p. 24.

Distomum fellis Olsson, Jacoby, "Beitr. z. Kenntnis. einig. Distomen," in 'Arch. f. Naturg.,' lxvi (1) (1900), pp. 12–16, pl. ii, figs. 8–12.

? Fellodistomum incisum (Rud.) Stafford, "Trematodes from Canadian Fishes," in 'Zool. Anzeig.,' xxvii (1904), p. 486.

This species has already been recorded from the east coast of Britain by Miss Lebour. It is a remarkably frequent parasite of the cat-fish (Anarrhichas lupus) being met with in almost every specimen, young and old. Its habitat is exclusively the gall-bladder. Fifty examples, at least, can usually be obtained from one host.

On the question of the identity of this species with two species found by Rathke[1] in Anarrhichas lupus and named by Rudolphi,[2] several authors have ventured an opinion. Van Benedin[3] considered D. fellis Olss. synonymous with D. incisum Rud. Stossich also evidently considered the two species identical, but retained Olsson's name. Jacoby repudiated the possibility of such identity. Stafford, leaving his reasons unexplained, adopts Rudolphi's name, and makes Dist. incisum Rud. the type of his genus Fellodistomum. How he identifies the species which he describes with Rudolphi's species is to me not very apparent. It has little in common with Rudolphi's description.

As regards D. incisum Rud. my opinion coincides with that of Jacoby. By no legitimate means can the form figured by Rathke and described by Rudolphi be made to agree with D. fellis Olsson. On the other hand, Rathke's second species, which Rudolphi[4] provisionally named Dist. anarrhichæ lupi, bears an undeniable resemblance to Dist. fellis.[5] The only description of this form, beyond its habitat and size, is contained in Rathke's words "corpore elongato carneo, apertura dorsali rotunda annulo luteo

[1] 'Dansk. Naturhist-Selsk. Skrivt.,' v (1799), p. 70, pl. ii, fig. 3.

[2] 'Entoz. Hist.,' ii (1), p. 361.

[3] 'Mém. Acad. Roy. Belg.,' xxxviii (1870), p. 48.

[4] 'Entoz. Hist.,' ii (1), p. 435.

[5] Olsson undoubtedly recognised this, for he marks D. anarrhichæ lupi as doubtfully identical with D. fellis. At the same time he completely ignores such a possibility in the case of D. incisum Rud.

cincta," but these words describe exactly the chief features which struck me when I removed my first specimens from the gall-bladder of their host. The thick, fleshy body extended vigorously towards both ends, the large knob-like ventral sucker (apertura dorsali), pale pink or flesh-like in colour and surrounded by a strikingly bright yellow ring contrasting strongly with the dull greenish hue of the rest of the body. These appearances are lost on preservation, and it was on this account, I believe, that Jacoby, who examined preserved material, was not impressed with Rathke's description. A most potent objection to the identification of Dist. anarrhichæ with D. fellis is the difference in habitat, for Rathke's specimens occurred in the stomach. Various hypotheses might be advanced to meet this difficulty, but it makes no difference to the matter in hand, for, as Looss has explained, such names as D. anarrhichæ lupi were not intended by Rudolphi as specific names, so that the name D. fellis Olsson remains good.

With regard to Stafford's specimens, the ovary is described on the left side and the testes as large and spherical. According to Jacoby's observations, which I confirm, the ovary always lies on the right side and the testes are obliquely oval in Distomum fellis. This renders it doubtful if Stafford's specimens are really identical with D. fellis, but it is possible that Stafford's statements may be due to a slip of the pen.

My adult specimens measure 2·5–3·3 mm. in length and 1·1–1·6 mm. in breadth. The normal breadth seems therefore to be about half the length, but the animal is capable of considerable extension. In the contracted state the breadth may almost equal the length and the animal becomes nearly globular. The shape in the quiescent state is most probably that represented by Jacoby. The body is thick and nearly opaque.

Numerous immature specimens were found, and these measured 1·1–2·5 mm., so that in this species maturity is reached at a size of about 2·5 mm.

As already mentioned the large ventral sucker surrounded by a yellow ring is the most prominent feature seen on ventral view. On the dorsal aspect the two intestinal diverticula show up very conspicuously by reason of their dark green contents.

The oral sucker is sub-terminal and globular, measuring ·40–·45 mm. The ventral sucker is also globular, situated a little behind the centre of the body. Its aperture may be either circular, transverse or diamond-shaped. Its diameter is ·9–1·0 mm., therefore about twice that of the oral sucker. Although of such great size, it is deeply sunk into the body and does not project much above the surface.

The histological structure of the suckers, especially the ventral sucker, presents many features of interest, and here my observations do not entirely agree with those of Jacoby. There are three chief varieties of cells: First, the large myoblasts (fig. 14, G z). These are extremely few, not more than two or three appearing in any one section. They are very large cells, measuring ·03–·05 mm., and, as Jacoby observed, the cell-body stains homogeneously deep red. The nucleus is central and oval in shape, measuring about ·02 by ·015 mm. It is traversed by a well-defined chromatin network, in the midst of which is situated a globular nucleolus, the diameter of which is ·007 mm. This type of cell differs from the myoblasts usually met with in other species, or at any rate in the species which I have hitherto examined, chiefly in the denser character of the nucleus and its shape.

These cells, however, have the same situation as the myoblasts in other species, namely, the median zone, midway between the outer and inner limiting membranes of the sucker.

The second variety of cell (fig. 14, D z s) is that identified by Jacoby as the cells which Schwarze[1] considered as "Reste der ursprünglichen Bildungszellen." These are the cells marked "G z" in Jacoby's figures, and they occur chiefly, if not exclusively, round the aperture of the sucker. They

[1] "Die postembryonale Entwicklung der Trematoden," in 'Zeitsch. f. wiss. Zool.,' xliii (1886), p. 54.

are large, rounded, oval cells, measuring ·045 by ·03 mm. They present a distinct cell wall, loosely granular contents and a small, dense nucleus, measuring ·006 mm. The nucleus stains dark red and the cell contents light purple with hæmalum-eosin. Jacoby's opinion of these cells is highly improbable. In reality they appear to be true cutaneous glands. Their marked resemblance both in shape and staining properties to the true subcutaneous glands, which in this species occur not only in front of, but also behind the ventral sucker, cannot be ignored. This, together with their distinctly marginal situation, if not a positive proof of their glandular nature, is at least strong evidence in favour of such a supposition. In addition it should be noted that these cells are smaller and less numerous in the oral sucker and are entirely absent from the pharynx.

The third variety of cell really consists of at least three different kinds. The first of these (fig. 14, P z) is confined to the outer zone, i.e. immediately beneath the outer membrane of the sucker. Their nuclei are small, dense, round bodies, measuring ·008 mm. The nucleoli are small and inconspicuous. The cell-body is usually fairly definite and of granular structure. The second kind (fig. 14, M z) occupies the median zone with the myoblasts. Their nuclei are invariably oval, and measure ·0115 by ·008 mm. They stain lightly and their chromatin granules are arranged peripherally. The nucleoli are always distinct. No trace of cell-body, however, can be detected with ordinary staining methods. The third kind (fig. 14, I z) lies in the inner zone. They are distinctly multipolar, and in a tangential section their fibrils can be seen anastomosing with each other. The cell-body takes on a deeper hue than any of the other cells, almost purple. They measure ·02 to ·03 mm., and their nuclei, which are small, dense and usually oval, measure ·007 by ·006 mm.

As to the function of these last three kinds of cells any expression of opinion would be hazardous. Many authors have advanced theories as to their nature, but without any

generally accepted conclusion. There is evidently scope for further investigation on the matter.

The foregoing observations apply mainly to the ventral sucker. In the oral sucker the cells are more closely packed and not so easily differentiated. It is also worth mentioning that in some specimens the marginal cells, to which I have ascribed a glandular function, can hardly be distinguished. These are generally highly contracted specimens. In most cases, however, these cells stand out with striking distinctness and give sections of the sucker an entirely unique appearance.

In spite of their large size the suckers are not particularly muscular. The fibres are widely separated and the interspaces are filled with a large amount of loose tissue. The radial fibres have a diameter of about ·001 mm. in the case of the ventral sucker. Two layers of circular fibres are present under both the external and internal surfaces.

The surface of the body is covered with a fairly uniform cuticle, ·002–·004 mm. thick; Jacoby says ·0113, but that is certainly too high a figure. There are no spines, but the cuticle is covered throughout its whole extent with curious little rod-like bodies, measuring ·004 by ·001 mm. (fig 13, Cu.). These are regularly arranged, close together, and stand out straight from the surface, not sloped backwards in the manner of spines. They are purely superficial outgrowths and do not penetrate the cuticle. It is strange that no mention is made of these by Jacoby, for their appearance is certainly remarkable enough. It may be that they are of transitory occurrence, but they were present in every specimen which I sectioned. The cuticle lining the suckers and the pharynx also shows these rod-like bodies in many specimens.

In the anterior part of the body the cuticle is thrown into numerous small transverse wrinkles. These are not the irregular wrinkles so commonly met with in other species; they are fairly uniform in size, and in longitudinal section present the appearance of a series of regular furrows. Of this, again, no mention is made by Jacoby. In the posterior part of

the body the cuticle does not display the same wrinkling, and it is not present on the dorsal surface of the body. The little rod-like bodies follow the course of these wrinkles, as do also the circular subcutaneous muscle-fibres. The longitudinal muscles, however, do not; their course is straight and it is evidently to their action that the wrinkling is due.

The diameters of the circular, longitudinal and diagonal muscle-fibres are respectively about ·0015 mm., ·003 mm. and ·004 mm., and the spaces separating them are on an average ·0035 mm., ·007 mm. and ·008 mm. in the three cases. The angle made by the diagonal fibres is about 135°. The myoblasts in connection with these fibres are quite as numerous as usual.

The true subcutaneous glands are large and numerous; they occur only on the ventral surface, but they are not confined to the anterior part of the body as is the case in most species. A considerable number are to be found behind the ventral sucker, but they cease about the middle of the post-acetabular region. They measure about ·045 by ·03 mm., and are rounded, oval in outline with highly granular contents and small eccentric nuclei, ·007 mm. in diameter.

Alimentary System.—There is a short pre-pharynx, in the wall of which well-marked circular and longitudinal muscle-fibres are present. The pharynx has a length of ·16–·21 mm.; its breadth is usually somewhat less. It appears to be more muscular than the suckers, for in addition to the usual fibres several equatorial fibres are present. It contains very few cells, and these are almost entirely of the myoblast type, situated in the middle zone, but much smaller than those of the ventral sucker.

There is practically no undivided œsophagus, the bifurcation taking place immediately behind the pharynx, but the initial parts of the diverticula are not lined with intestinal epithelium. Each of these parts is about ·1 mm. long and ·04 mm. wide. They are lined by a cuticularised membrane. The diverticula are simple wide sacs running nearly the whole length of the body, but terminating at the posterior

end of the testes. Anteriorly their width is about ·2 mm. but further back they dilate to ·3 mm. They are situated just below the dorsal surface of the body. The intestinal epithelium is exceptionally well marked. It is cubical or columnar in type, but the cells are all of different sizes and shapes, projecting to various degrees into the lumen. Towards the posterior end of the diverticula the cells are usually flatter. It is evident that these cells are capable of considerable pseudopodial movement, for they contain varying amounts of bile which they have ingested (fig. 14, z). The extended cells contain a large amount of bile surrounded by a vacuole. As the bile becomes metabolised and absorbed the cell contracts and the vacuole disappears. Two neighbouring cells may thus present a great contrast, one being highly extended and packed full of bile, the other small, flat and without any trace of bile. From this there can hardly be any doubt that the cells actually engulph the intestinal contents. In their extended state they may reach a length of ·04 mm. They possess small round nuclei situated basally. The hair-like or thread-like processes so frequently described in other species are entirely absent in this, and it appears as if the character of the epithelium and the manner of food absorption in this species were different from that in most other species. Here, however, the dark-green colour of the intestinal contents renders its presence within the epithelial cells a matter of easy observation—a fact which is by no means so easy to demonstrate in those species in which the intestinal contents are colourless or nearly so. It appears highly probable that in many cases a certain restricted pseudopodial movement of the epithelial cells does really take place, but it is a quite as well attested fact that in many other cases no such movement occurs, and that the process of assimilation of material, partially metabolised in the lumen of the intestine, is effected by a capillary action of the hair-like processes of the epithelial cells.

Excretory System.—The vesicle is of the Y-shaped type. The main stem is short and almost diamond-shaped, its length

being about ·2 mm. and greatest breadth ·1 mm. It lies between the two testes and bifurcates at their anterior border. The limbs pass round the sides of the ventral sucker and take up a position immediately ventral to the intestinal diverticula. They run forward as far as the level of the pharynx, and their ends occupy a position about midway between the pharynx and the margins of the body. The whole vesicle, both stem and limbs, is lined by a well-marked epithelium, the individual cells of which in many cases stand out prominently and can be easily observed (figs. 13, 14, Ex.). At other places they are flattened and not so distinct, so that here, again, we are evidently dealing with cells which are able to change their shape in some degree. The nuclei of these cells are oval and measure about ·01 by ·008 mm. The vesicle communicates with the exterior by a short narrow muscular tube, around which are numerous nucleated cells. The excretory aperture is at the posterior end of the body.

Genital System.—The genital aperture is situated on a large papilla, which is seen prominently on external inspection. It lies immediately in front of the ventral sucker, and displaced well to the left of the middle line. At first sight the genital sinus appears to be of great size, but this is due to a wide expansion of the ductus ejaculatorius. In reality the genital sinus is comparatively small.

Male Organs.—The testes are two oval bodies symmetrically placed about midway between the ventral sucker and the posterior end of the body. Their long axes are oblique, the posterior end being nearer the middle line; they are separated by the breadth of the excretory vesicle. They are distinctly ventral in position, lying under the ends of the intestinal diverticula. Their average dimensions are ·45 by ·19 mm., and the thickness equals the breadth. The vas deferens arises from a little nodule about the middle of their inner surface.

The vasa deferentia unite in a small bipartite vesicula seminalis, both parts of which are enclosed within the cirrus-pouch. Jacoby failed to note this bipartite condition, but

there is no doubt it invariably occurs. The posterior part is the smaller of the two. Each has a length of about ·085 mm.; the breadth, which is capable of great variation, is respectively ·06–·11 mm. and ·04–·08 mm. The walls are muscular, and an epithelial lining with a few large nuclei can be observed. The pars prostatica is exceedingly well developed, and, in fact, occupies the largest portion of the cirrus-pouch. It has, as represented in Jacoby's figure, a bulbous shape, narrowed somewhat at its junction with the vesicula seminalis. Its length is ·18 mm. and greatest breadth ·13 mm. Its wall is muscular and it is lined by a distinct epithelium with oval nuclei, measuring ·0096 by ·0057 mm. The lumen is almost entirely filled by long string-like masses of prostatic secretion, which lie, like so many filaments, parallel to each other, and are directed out towards the ductus, into which they project. The prostatic cells occupy a large part of the cirrus-pouch, surrounding the pars prostatica and the vesicula seminalis. A few are also found around the ductus. Their nuclei measure ·008–·01 mm. Amidst the prostatic cells several large myoblasts or ganglion cells occur. They are distinguished by their much larger nuclei (·012 mm.) and different staining reaction. The pars prostatica passes into a wide (·11 mm.) ductus ejaculatorius, of comparatively short length. Its wall has an irregular outline, being crumpled up in somewhat the same manner as in Brachycladium oblongum, but not nearly to the same extent or so regularly. At first sight it might be mistaken for the sinus genitalis, and it certainly offers a contrast to the long narrow ductus found in the majority of Distomids. It is doubtful if it functions as an eversible cirrus, but if so it evidently cannot be everted to any great length. It was not everted in any of my specimens, and Jacoby makes no mention of having seen it in such a condition. The extreme prominence of the genital papilla may be an adaptation to compensate for the shortness of the cirrus. The walls of the ductus have the usual structure, but are unusually thick. The lining consists of a thick metamorphosed epithelium easily distinguished from the cuticular

lining of the sinus genitalis. A small number of "Begleitzellen" surround the ductus.

Female Organs.—The ovary is situated on the right side of the body immediately in front of the testis, and just behind the ventral sucker. Its shape is not "kegelförmig," as Jacoby describes it, but multilobate, the lobes having apparently no uniform arrangement. This confirms Stafford's observation. It is elongated in a direction parallel to the long axis of the testis, alongside which it lies, and it appears to be a little less than the testis in size. The oviduct arises from its anterior surface and passes behind the ventral sucker towards the dorsal surface. It dilates somewhat before giving off Laurer's canal, and then bends forwards to receive the yolk-duct and pass into the ootype. Laurer's canal is a tube of about ·02 mm. diameter, which runs with several small convolutions to open on the middle line of the dorsal surface on the level of the posterior border of the ventral sucker, or a little in front of that. It is surrounded throughout its whole course by numerous small cells. There is no true receptaculum seminis.

The yolk-glands are very limited in extent. They are exclusively lateral, lying to the outer side of, or even slightly ventral to, the ventral sucker. They extend from a little in front of the ventral sucker to near its posterior border. The follicles are few and of small size, and the cells have a great affinity for hæmatoxylin stains. The yolk-ducts run back alongside the intestinal diverticula, and unite in a small median receptacle situated at the level of the anterior end of the testes.

Around the ootype and oviduct there is a fairly compact shell-gland of small size, but with numerous cells, the bodies of which do not stain readily, but the nuclei are very prominent. The latter are oval and about ·005 mm. in size. The ootype passes forwards into the uterus, which describes numerous convolutions dorsal to the ventral sucker. The vagina runs straight along the anterior surface of the ventral sucker and opens into the genital sinus. The initial part of

the uterus (about a third of its length) is filled with numerous sperms, and functions as a receptaculum seminis uterinum. The ova are moderate in number and of small size. They are narrow oval in shape, with thick, tough shell, and measure ·0424 by ·0231 mm.

Fellodistomum agnotum n. sp., Pl. 10, fig. 15.

Among the Distomids which were obtained from the gall-bladder or the adjoining part of the duodenum of Anarrhichas lupus, there occurred a few which resembled Fellodistomum fellis so closely that they were included along with it. On later and more careful examination, however, they showed features which rendered their specific distinction comparatively easy. My attention was first directed towards these specimens in the course of investigating the size at which Fellodistomum fellis attained maturity. It was rather disconcerting to find that some small specimens had numerous ova, while other larger specimens were quite immature. As events have proved, the smaller specimens belong to a distinct species.

Under these circumstances it is difficult to say what the exact habitat of this new species is. As far as my recollection goes, however, these were the specimens which occurred in the duodenum, and the true Fellodistomum fellis is apparently confined to the gall-bladder. Unfortunately no further opportunity has offered of confirming this. The new species displays the same green-coloured intestinal diverticula so characteristic of Fellodistomum fellis, but this might easily be due to bile ingested in the duodenum.

The chief diagnostic features of the new species are the more elongated body, smaller and less prominent ventral sucker, the forward position of the yolk-glands, and the backward prolongation of the uterus. It is much less numerous than F. fellis in the proportion of 1 to 30.

The largest specimen had a length of 3·3 mm. and a

breadth of ·87 mm. Other specimens were not quite so attenuated, but the breadth is rarely more than one third of the length. Immature specimens were found up to 1·05 mm. in length. The body usually tapers considerably towards each end. The oral sucker measures ·34 mm. and the ventral sucker ·51 mm. in a specimen 3 mm. long. The proportion is constantly 2 : 3 instead of 1 : 2 as in F. fellis. Both suckers are globular. The ventral sucker lies a little in front of the middle of the body.

The alimentary system resembles that of F. fellis. The pharynx is somewhat smaller—·15 by ·12 mm. The œsophagus is practically absent. The diverticula extend along the sides of the body and terminate at the posterior border of the testes, therefore at a considerable distance from the posterior end of the body. This feature is evidently shared by the genus in common with the genus Steringophorus, although it is not apparent at first sight in the case of Fellodistomum fellis, in which the testes are placed very near the posterior end of the body.

The excretory system corresponds with that of F. fellis, but the main stem of the vesicle is much elongated.

The genital aperture is placed on a prominent papilla in the same situation as in F. fellis, and the cirrus-pouch has the same structure. The testes are situated not far behind the posterior border of the ventral sucker, and at a considerable distance from the posterior end of the body. They have the same shape and disposition as in F. fellis. The ovary has also the same situation. The yolk-glands, however, lie entirely in front of the ventral sucker and extend along the sides of the body from the anterior border of the sucker to the level of the pharynx or intestinal bifurcation. They form a broader and more compact group than do those in F. fellis. The uterus describes a few windings in front of the testes, then runs back between them very nearly to the posterior end of the body. In this part it forms a single descending and ascending loop with little or no convolution. On again reaching the level of the ovary it makes

several irregular convolutions dorsal to the ventral sucker and thence proceeds to the genital aperture. This backward prolongation of the uterus forms a ready means of distinguishing the species with the naked eye from F. fellis. The ova are somewhat larger than those of the latter species, measuring about ·048 by ·024 mm.

For the genus Fellodistomum, which Stafford has somewhat scantily characterised, the following definition may be offered :

Small to middle-sized forms with thick fleshy body, subcylindrical, tapering more or less towards each end. Cuticle thick and rough, but without spines. Oral sucker subterminal, simple. Ventral sucker about the middle of the body, larger than oral sucker, globular. Pharynx small, pre-pharynx short, œsophagus very short or absent. Diverticula, simple wide sacs terminating a little behind the testes. Excretory vesicle Y-shaped, the bifurcation taking place behind the ventral sucker and the limbs stretching far into the neck. Genital aperture situated on a prominent papilla to the left of the middle line immediately in front of the ventral sucker. Small genital sinus. Testes symmetrical, a moderate distance behind the ventral sucker. Cirrus-pouch compact, bulbous. Vesicula seminalis small, bipartite. Pars prostatica well marked ; ductus ejaculatorius short, wide, with walls thrown into irregular folds (in the retracted state). Ovary multilobate, situated just in front of the right testis. Receptaculum seminis absent; Laurer's canal present. Yolk-glands lateral, of very limited extent. Initial part of uterus functions as receptaculum seminis uterinum. Uterus restricted in extent, either confined between the testes and the genital aperture, or with a loop passing backwards between testes to the posterior end of the body. Ova small, thick-shelled, measuring ·04–·05 mm. by ·02–·025 mm.

Type.—Fellodistomum fellis (Olsson, 1868) = ? F. incisum (R.) Stafford. Including also F. agnotum n. sp.

Both Stafford and Odhner have noted a close resemblance between this genus and the genus Steringophorus Odhn.,

1904 (= Leioderma Stafford, 1904), of which the type is St. furciger (Olss., 1868). The latter genus has been efficiently characterised by Odhner.[1] The two genera show unmistakable evidences of relationship, and they represent a type of structure distinct from that of any other sub-family of the Prosostomata. They may therefore be regarded as the nucleus of a separate sub-family as already indicated by Odhner, and for this I propose the name Fellodistominæ n. subfam., with the following provisional diagnosis :

Under middle-sized to middle-sized forms with fleshy body. Cuticle unarmed. Ventral sucker larger than oral sucker, situated about the middle of the body. Alimentary canal with short or nearly absent œsophagus, and diverticula not extending much beyond the level of the testes. Excretory vesicle Y-shaped, the fork taking place behind the ventral sucker and the limbs extending well into the neck. Genital aperture a short distance in front of the ventral sucker, median or to the left side. Testes symmetrical, lateral, not far behind the ventral sucker. Cirrus-pouch compact, bulbous, containing a small bipartite vesicula seminalis, a well-marked pars prostatica, and a short, wide ductus ejaculatorius. Ovary in front of right testis, multilobate. Receptaculum seminis absent (or present sometimes), Laurer's canal present. Yolk-glands limited in extent, lateral, on each side of the ventral sucker. Yolk-reservoir median behind ventral sucker. Uterus more or less convoluted, confined between testes and genital aperture or extending back between testes into the posterior part of the body. Ova fairly numerous, measuring about ·04–·06 mm. by ·02–·03 mm.

Type, Fellodistomum (Stafford, 1904).

Including also Steringophorus, Odhner.

Genus, Steringophorus Odhner, 1904.

Steringophorus cluthensis n. sp., Pl. 10, fig. 16.

This species was found fairly abundantly in the upper

[1] "Trematoden d. arktischen Gebietes," in 'Fauna Arctica,' iv (1904), p. 309.

reaches of the intestine (duodenum and cæca) of Pleuronectes microcephalus, the lemon-dab, from the Firth of Clyde. It differs in several respects from St. furciger (Olss.), which is found so commonly in many Pleuronectid fishes in the North Sea.

In life the animal is capable of great extension and contraction, but on being killed or on being allowed to die in its natural habitat it assumes a fairly regularly oval outline, always more pointed towards the anterior extremity. It is considerably flattened and has a rather delicate, transparent appearance. Living specimens have a distinctly reddish colour, not so deep as that of St. furciger.

The length is 1·5–2 mm., but none of my specimens seem to be fully mature, so they may attain a larger size. The breadth is about two fifths of the length—·6–·8 mm. Cuticle unarmed. The oral sucker invariably lies a short distance from the extreme anterior end, and it is usually elongated in the long axis of the body. It measures about ·22 by ·15 mm. The ventral sucker is almost exactly twice as large, its diameter being ·44 mm. in a specimen of 2 mm. length. It is situated a little behind the middle of the body, and it this respect it differs from the position in St. furciger, in which it is in front of the middle of the body.

The pharynx is immediately behind the oral sucker and measures ·085 mm. in diameter. The œsophagus is twice as long as the pharynx, sometimes slightly more, sometimes a little less than that. This feature, again, distinguishes the species from St. furciger, in which the œsophagus is about the same length as the pharynx. The diverticula are simple and extend a little beyond the testes, but not so much as in St. furciger.

The excretory vesicle is perhaps the most obvious diagnostic feature. It is Y-shaped, but the unpaired portion is very short, so that it sometimes appears almost V-shaped. The paired limbs extend forward to the level of the pharynx. It is distinctly mapped out by the refringent nature of its contents, but is not so conspicuous as in St. furciger.

The genital aperture is situated just behind the intestinal bifurcation, to the left of the middle line, although not much. The testes are symmetrically situated midway between the ventral sucker and the end of the body. They are somewhat further back than in St. furciger. Their long axes are always a trifle oblique, the anterior end being directed outwards. They measure ·15 by ·12 mm. The cirrus-pouch is bulbous or nearly globular, and lies entirely in front of the ventral sucker. Its internal structure is the same as that of St. furciger, but the pars prostatica is longer and narrower, as are also the two parts of the vesicula seminalis.

The ovary is situated immediately in front of the right testis. It is multilobate, but very small. The yolk-glands are much more extensive than in St. furciger. They extend from the testes forward to the level of the middle of the cirrus-pouch, i.e. well in front of the ventral sucker. In St. furciger they do not reach the anterior border of the sucker. The transverse yolk-ducts run obliquely backwards to unite at the level of the anterior border of the testes in a small median yolk-reservoir. In none of my specimens was the uterus very voluminous. A few convolutions were found between the testes and stretching back to the posterior end of the body. The terminal part runs forwards on the left side of the ventral sucker to open into the sinus genitalis. The ova are not particularly thin shelled, and measure ·044–·056 by ·028–·032 mm.

The chief diagnostic features of this species may be summed up as follows: Post-acetabular region shorter than pre-acetabular region. Œsophagus twice as long as pharynx. Excretory vesicle nearly V-shaped. Yolk-glands extending in front of ventral sucker.

The introduction of this species within the genus Steringophorus involves only two modifications of Odhner's definition. The words "Saugnäpfe genähert" and "Stamm (der Exkretionsblase) gabelt sich zwischen den Hoden" should be deleted.

A species which bears a striking superficial resemblance to

Steringophorus cluthensis is Distomum pagelli v. Ben. ('Mém. Acad. Roy. Belg.,' xxxviii (1871), Pl. IV, fig. 17), from Sparus centrodontus. Van Beneden, unfortunately, gives absolutely no description of the species, but from his figure it seems probable that it is really a Steringophorus sp. It differs from Ster. cluthensis in having the ventral sucker three times as large as the oral sucker, the ovary globular, the yolk-glands extending behind testes, and the genital aperture further from the intestinal bifurcation.

It is evidently a somewhat difficult matter to differentiate Steringophorus generically from Fellodistomum. The features which require to be emphasised in the former are: (1) the presence of a distinct œsophagus; (2) the absence of a protuberant genital papilla; (3) the situation of the genital aperture near the intestinal bifurcation instead of close in front of the ventral sucker; and (4) the presence of a true receptaculum seminis.[1] These differences are not of great relative importance, and it is not at all impossible that the genera may eventually prove identical, in which case the name Steringophorus must be regarded as a synonym of Fellodistomum.

Sub-family Plagiorchinæ Pratt, 1902.

Genus Plagiorchis Lühe, 1899.

Plagiorchis notabilis n. sp., Pl. 10, fig. 17.

To the genus Plagiorchis have already been assigned well-nigh a dozen species, one or two of which can be differentiated from each other only with difficulty. They form on the whole a very homogeneous group. To these I have to add a form possessing such well-marked features that there can be no doubt of its specific distinctness.

[1] According to Odhner there is no receptaculum seminis, but Miss Lebour ('Fish Trematodes of the Northumberland Coast,' p. 15) has shown that such a structure may actually exist in Steringophorus furciger.

The species in question was first obtained on August 21st, 1907, from the middle part of the intestine of Anthus obscurus (rock pipit), which is by far the commonest bird inhabiting the rocks along the shore in this district. The parasite, however, is by no means frequent, for out of eleven pipits shot during August to October only two specimens were obtained—one adult and one immature. A point of interest is that the two birds from which those specimens were obtained contained several other parasites, in particular two species of Spelotrema and a number of Cestodes. The other birds contained only a few examples of Spelotrema claviforme and an occasional Cestode. Several other rock-frequenting birds, e.g. Saxicola œnanthe and Motacilla flava, were examined in the hope of finding more specimens of the parasite, and towards the middle of October another single example was found in the intestine of Motacilla. This second example did not entirely agree with the first, but at present they may be regarded as one and the same species. To avoid detailed comparison the specimen from Anthus will first be described, and the main features of difference in the specimen from Motacilla will then be indicated.

The general shape is that common to the genus. The length is 1·6 mm.; the breadth is fairly uniform—·52–·57 mm. Almost the whole surface of the body is covered with minute straight spines which have the peculiarity that they just barely pierce the cuticle. This feature is shared by the other members of the genus, and would appear to be characteristic.

The oral sucker is not quite at the extreme anterior end of the body, but is a short distance from it. Its length is slightly greater than its breadth, and it has an elongated slit-like aperture. This again appears to be characteristic of the genus. In this species the aperture is slightly expanded posteriorly and narrows to a fine point at the anterior end. The sucker measures ·20 by ·18 mm. The ventral sucker is globular, with a circular aperture, and measures only ·16

mm. It is situated at the end of the first third of the body length.

The pre-pharynx is extremely short; the pharynx is broad and measures ·07 by ·09 mm. There is practically no œsophagus and the simple straight diverticula extend to within a short distance of the posterior end of the body.

The genital aperture lies immediately in front of the ventral sucker, median or very slightly to the left. The cirrus-pouch bends round to the right side of the ventral sucker. It differs in shape from that of most members of the genus, approaching most nearly that of Plagiorchis (Lepoderma) ramlianus (Lss.). It is short and stout and does not extend beyond the posterior border of the ventral sucker. It is somewhat pointed at its proximal end, where it receives the vas deferens. The vesicula seminalis is oval with only the slightest trace of a constriction, and measures ·14 by ·07 mm. The prostate cells are fairly numerous, surrounding the first half of the ductus ejaculatorius and pars prostatica. In this specimen the cirrus was exserted as a long, narrow, sinuate filament, pointed at the end and measuring ·25 mm. in length. The vagina runs up to the genital aperture on the left side of the ventral sucker. The arrangement of the genital glands is the same as that in the other members of the genus. The anterior testis is ·20 mm. behind the ventral sucker, and the posterior testis is ·35 mm. from the posterior end of the body. Between the testes there is a space of ·1 mm. They are about equal in size, measuring ·25 by ·16 mm. They are elongated in the long axis of the body, and they lie to the inner side of the intestinal diverticula.

The ovary is situated further forward than in any other species of the genus. It lies on the right side with its anterior border contiguous with the end of the cirrus-pouch, or on the level of aperture of the ventral sucker. It also lies to the inner side of the right intestinal diverticulum, but slightly overlaps it. It is longitudinally oval and measures ·16 by ·12 mm. From its inner side the oviduct arises and runs towards the middle of the body, where it gives off

Laurer's canal. No receptaculum seminis could be made out with certainty.

The yolk-glands are almost entirely confined to the sides of the body and extend from the pharynx to the posterior end. They do not unite in the middle line posteriorly, but a few follicles stretch across the body just behind the pharynx. The intestinal diverticula are overlapped to a slight extent, especially posteriorly. The transverse yolk-ducts pass a little in front of the anterior testes to unite in a small reservoir.

The uterus is confined to the posterior half of the body and does not overlap the intestinal diverticula. Its course is typical of the genus, but it differs in being more voluminous in front of the posterior testis than behind it. It does not overlap the testes. The ova are not very numerous; they measure ·031 by ·019 mm. and have a bright yellow shell.

The chief diagnostic features of this species are therefore the short cirrus-pouch and the forward position of the ovary.

The specimen from Motacilla flava was smaller and slightly narrower; length 1·4 mm. Oral sucker ·17 by ·16 mm.; aperture ·09 by ·03 mm.; thickness of wall ·03 mm. Ventral sucker two fifths of the body length from the anterior end, size ·14 by ·13 mm.; aperture circular. Pharynx ·054 by ·069 mm. Spines ·0096 mm. long.

Cirrus not completely exserted. Vesicula seminalis distinctly bipartite, with a small anterior and a larger posterior part; combined length of the two parts ·066 mm. The distinct bipartite condition of the vesicula in this specimen is one reason for doubting if it is really identical with the specimen from Anthus obscurus. Possibly the difference in the state of exsertion of the cirrus may account for the variation in the vesicula.

The genital glands have much the same situation as before, but the posterior testis is only ·12 mm. from the end of the body and the anterior testis ·13 mm. behind the ventral sucker. They are smaller and not so elongated, ·17 by

·15 mm. and ·19 by ·15 mm. respectively. The ovary is also smaller—·115 by ·105 mm. The uterus is more voluminous behind the posterior testis and overlaps the testes to a slight extent. The ova are brownish-yellow and measure ·0308 by ·0193–·0212 mm. The length is practically invariable, but one abnormally large ovum was observed in the posterior loop of the uterus, measuring ·0327 by ·0212 mm. The average size may be taken as ·031 by ·021 mm. They are not truly ellipsoidal, there being a slight flattening on one side, which probably accounts for the variation in the breadth. The shell has a thickness of ·0008 mm. The vagina lies on the right side of the ventral sucker and extends as far back as its posterior border. It is marked off from the uterus by a distinct constriction. Its diameter is ·015 mm. and its walls are ·006 mm. thick.

The yolk-glands are less voluminous than in the first specimen. They are entirely lateral and extend only a short distance in front of the ventral sucker. This might be ascribed to imperfect development, but as both specimens were fully mature it seems more reasonable to allow that some variation may occur in the extent of the yolk-glands. In this respect Braun,[1] in discussing the distinction between Pl. elegans (R.) and Pl. cirratus (R.), remarks that much weight cannot be placed on the relative extent of the yolk-glands, for they vary even in examples from the same host.

This specimen differs from the first mainly in the condition of the vesicula seminalis, the extent of the yolk-glands, and the size of the genital glands. Until more material is available it is impossible to say whether these features are of specific importance or merely variations.

The species which follow are introduced mainly for the purpose of presenting figures which were omitted from a previous paper.[2] Little opportunity has offered of making

[1] "Fascioliden der Vögel," in 'Zool. Jahrb.,' syst. xvi, pp. 37–55, pl. iii, figs. 25–34a.

[2] "Observations on the Trematode Parasites of British Birds," in 'Annals and Mag. Nat. Hist.' (7), xx (1907), pp. 245–271

fresh investigations in connection with these species, and the notes which are herewith given are only such as to correct a few obvious errors.

Sub-family, Microphallinæ Ward, 1901.

Genus, Spelotrema Jägersk., 1900.

This genus includes the species Sp. pygmæum (Levin.), Sp. claviforme (Brandes) Mihi., Sp. simile Jägersk., and Sp. excellens Mihi. A fifth species, namely, Sp. feriatum Mihi, has been found to belong to the nearly allied genus Levinseniella. The genus may require to be further restricted to three species, for Sp. claviforme (Brandes) Mihi is only doubtfully distinct from Sp. pygmæum. The characters of the four species may be briefly summarised as follows:

Spelotrema pygmæum (Levins.) Odhn.

Odhner, "Trematoden des arktischen Gebietes" in 'Fauna Arctica,' iv (1904), pp. 315–317, fig. 1, 2A.

Length ·3–·5 mm. Maximum breadth ·2–·3 mm. Club-shaped. Diameter of suckers about ·04–·05 mm., but oral sucker always slightly larger than ventral sucker. Ventral sucker a third of the body length from the posterior end. Intestinal diverticula reaching posterior border of ventral sucker. Genital body only half the breadth of the ventral sucker. Ductus ejaculatorius short and direct. Testes comparatively large. Uterus fairly voluminous, but not obscuring testes. Ova ·021–·023 by ·012 mm. Habitat, Somateria mollissima, Somateria spectabilis, Oidemia nigra, and Oidemia fusca.

Spelotrema claviforme (Brandes) Mihi (Pl. 10, fig. 18).

Nicoll, "Trematode Parasites of British Birds" in 'Annals and Mag. Nat. Hist.,' (7) xx, (1907), pp. 254–255.

Length ·2–·4 mm. Maximum breadth ·15–·20 mm. Club-

shaped. Oral sucker always distinctly larger than ventral sucker; diameters ·035–·04 mm. and ·03–·035 mm. respectively. Ventral sucker less than a third of the body-length from the posterior end. Intestinal diverticula short, wide apart, and do not reach the level of the ventral sucker. Genital body less than half the diameter of the ventral sucker. Ductus ejaculatorius short and direct. Testes not prominent. Uterus voluminous, obscuring the testes and extending slightly in front of ventral sucker. Ova ·020–·024 by ·011–·014 mm. Habitat, Pelidna alpina, Ægialitis hiaticula, Anthus obscurus,[1] Numenius arquata,[1] Motacilla flava,[1] Larus ridibundus.[1]

Spelotrema simile Jägersk.

Jägerskiöld, "Levinsenia pygmæa Levinsen, etc.," in 'Centralbl. f. Bakter.,' Abth. i, Bd. xxvii (1900), pp. 732–740.

Length ·4–·6 mm. Maximum breadth ·2 mm. "Biscuit-shaped." Oral sucker slightly smaller than ventral sucker, diameter ·05–·06 mm. Intestinal diverticula reach posterior border of ventral sucker. Genital body has diameter at least two thirds that of the ventral sucker. Ductus ejaculatorius long and convoluted. Uterus not usually voluminous, not obscuring testes or yolk-glands. Ova pale, measuring ·023–·026 by ·011–·013 mm. Habitat, Larus argentatus, Larus fuscus, Larus ridibundus.[1]

Spelotrema excellens, Mihi (Pl. 10, fig. 19).

Nicoll, 'Annals and Mag. Nat. Hist.,' (7) xx, (1907), pp. 248–251.

Length ·7–1·4 mm. Maximum breadth ·35–·50 mm. Club-shaped. Oral sucker slightly larger than ventral sucker; diameter ·06–·085 mm. Intestinal diverticula terminate at the level of the centre of the ventral sucker. Genital body nearly as large as ventral sucker. Ductus ejaculatorius short and straight. Uterus very voluminous, obscuring testes, but not extending in front of ventral sucker as a rule. Ova

[1] New hosts

very numerous, measuring ·023–·025 by ·010–·013 mm. Habitat, Larus argentatus.

Genus, Levinseniella Stiles, 1902.

The species of this genus, namely L. brachysoma (Crepl.), L. pellucida Jägersk., and L. propinqua Jägersk., have been efficiently described by Jägerskiöld.[1] The species which I have described under the name Spelotrema feriatum n. sp.[2] must be considered as a mixture of two or more of the above mentioned species or of some hitherto undescribed species of the same genus. I found the species originally in Hæmatopus ostralegus, and was struck with its resemblance to Distomum brachysomum Crepl., but was led astray by Villot's transposed representation[3] of Creplin's species. Jägerskiöld's elucidation of the true structure of that species has enabled me to identify my specimens as Levinseniella brachysoma or some nearly related species.

At the time of describing the species "Spelotrema feriatum," I entertained great doubt as to the actual identity of my specimens from Vanellus and Hæmatopus with those from Pelidna and Ægialitis. This doubt has now given place almost to a certainty that they are distinctly different, for the former, although quite as large as the latter, were in every case decidedly immature and pale in colour, while the latter contained numerous ova and were of a more or less brownish colour. According to Jägerskiöld, Hæmatopus harbours a species distinct from that inhabiting Ægialitis, Totanus and Pelidna. This would appear to solve the difficulty with regard to my specimens, but unfortunately I cannot entirely reconcile my own observations with Jägerskiöld's descriptions. For instance, the brown pigmentation of the body and the intensely black mapping

[1] "Zur Kenntniss der Trematodengattung Levinseniella," in 'Zool. Studien tillägnade,' Prof. T. Tullberg, 1907, pp. 133–154.

[2] 'Annals and Mag. Nat. Hist.' (7), xx, pp. 251–253.

[3] 'Ann. d. Sciences Nat.' (6), viii (1879), pp. 22–24, pl. v, fig. 7.

out of the excretory system are not mentioned by Jägerskiöld I have endeavoured to utilise the table of specific differences given by Jägerskiöld[1], but without any consistent result. From the point of view of the comparative length of the pre-pharynx, for instance, my specimens from Totanus and Vanellus ought to be regarded as L. propinqua but the identity is not confirmed in other respects. For the present it seems the safest plan to refer my specimens from Pelidna, Ægialitis and Totanus to Levinsinella brachysoma (Crepl.), while those from Hæmatopus and Vanellus must be regarded as Levinsinella sp. inquir. The most curious feature about the latter is the fact that on no occasion did I find a fully mature specimen, although I examined several of these birds at different times. In addition to the foregoing hosts I have also to add Numenius arquata, in the cæca of which I have found a Levinsinella sp., probably L. brachysoma.

Sub-family Tocotreminæ Jägerskiöld, 1902.

Genus Tocotrema Looss, 1899.

Tocotrema jejunum Mihi (Pl. 10, figs. 20 and 21).

I have not yet again met with this species. Two figures of it are shown here, one representing what may be regarded as the normal shape, the other that in which it was usually found.

Genus Cryptocotyle (Lühe) Mihi, 1907.

Cryptocotyle concava (Crepl.) (Pl. 10, figs. 24 and 25).

My revised definition of this genus requires alteration in, at least, one point. From a rather poor series of sections I have been able to make out that the genital sucker contains a distinct plug-shaped body ("kegelförmiger Körper"). It is, however, much smaller than the corresponding structure

[1] Op. cit., p. 147.

in Tocotrema. This fact removes an important point of distinction between the genera Cryptocotyle and Tocotrema, but sufficient differences remain to keep them generically separate.

In my previous note on Looss's sub-family Cœnogoniminæ (Heterophyinæ), I arrived at practically the same conclusion as Jägerskiöld did in a paper[1] which I had not at that time seen. Jägerskiöld separates the sub-family Tocotreminæ from the Cœnogoniminæ, including in the former the same genera, with the exception of Cryptocotyle, as I did later. He also ventures the supposition that the Microphallinæ are more or less nearly related to the Tocotreminæ-Cœnogoniminæ group, and this seems not at all unreasonable. Their relation to the Brachycœliinæ is undoubtedly much more remote, and my suggestion of a natural family to include all these forms was certainly premature if not erroneous.

Sub-family Gymnophallinæ Odhn., 1904.

Genus Gymnophallus Odhn., 1900.

Gymnophallus dapsilis Mihi (Pl. 10, fig. 24).

An explanation of the curious condition of the ova in this species is suggested in a note by Looss,[2] who has met with an analogous condition in several other species, and ascribes it to an imperfect functioning of the ootype. The malformed ova may therefore in a sense be regarded as abortive. I have since noted the condition in one or two other species, but only in isolated individuals, and never with the same remarkable frequency as in Gymnophallus dapsilis.

Sub-family Maritreminæ provis.

Genus Maritrema Mihi, 1907.

I have at present nothing further to add to the descriptions

[1] "Scaphanocephalus expansus (Crepl.), etc.," in 'Results of Swedish Zool. Exped. to Egypt,' 1901, No. 23.

[2] "Trematoden aus Seeschildkröten," in 'Zool. Jahrb. Syst.,' xvi. p. 475.

of the three species of this genus. They are represented here in Pl. 10, figs. 25–27.

Dr. Jägerskiöld has just sent me a paper dealing with the genera Spelotrema and Maritrema (in 'Centralbl. f. Bakt., etc., I Abt. Originale,' Bd. xlviii, pp. 302–317). His description of Spelotrema excellens appears to agree very closely with mine. The elongated shape of the ovary is certaintly not a constant feature of the species, nor is the large size of the vesicula seminalis, on which Jägerskiöld lays some weight. It is an organ which is capable of not a little variation in size at different times in the same animal.

With regard to the genus Maritrema, Jägerskiöld's two new species appear to be quite distinct from those which I have previously described. He is correct in drawing attention to the disposition of the yolk-glands. The genus, as Jägerskiöld points out, shows a relationship to the Microphallinæ, but it is certainly not close enough to permit of its being included in that sub-family.

EXPLANATION OF PLATES 9 AND 10.

Illustrating Dr. William Nicoll's paper entitled "Studies on the Structure and Classification of the Digenetic Trematodes."

The following letters apply to all the figures:

B.S. Ventral sucker. *C.B.* Cirrus-pouch. *D.E.* Ductus ejaculatorius. *D.St.* Yolk-glands. *Ex.* Excretory vesicle. *J.* Intestinal diverticula. *K.St.* Ovary. *L.C.* Laurer's canal. *M.S.* Oral sucker. *Oe.* Œsophagus. *Ov.* Ova. *P.G.* Genital aperture. *Ph.* Pharynx. *P.Ph.* Pre-pharynx. *P.Pr.* Pars prostatica. *Pr.* Prostate glands. T_1,T_2. Testes. *R.S.* Receptaculum seminis. *S.D.* Shell-gland. *Ut.* Uterus. *Vg.* Vagina. *V.S.* Vesicula seminalis.

Fig. 1.—Stephanophiala laureata (Zed.). Ventral view. × 35. *V.P.* Ventral papilla.

Fig. 2.—Steph. laureata. Longitudinal section of anterior end, nearly median. × 85. *V.P.* Ventral papilla. *D.P.* Dorsal papilla. *a.* Myoblast.

Fig. 3.—Steph. laureata. Cirrus-pouch and vagina. Somewhat diagrammatic. × 270. ♂. Male genital aperture. ♀. Female aperture.

Fig. 4.—Steph. laureata. Transverse section, yolk-follicles. × 270. *P.C.* Parietal cell. *C.C.* Central cell. *D.G.* Yolk-duct. *Y.C.* Yolk-cell.

Fig. 5.—Steph. laureata. Immature specimen. × 60. *E.S.* Eye spot.

Fig. 6.—Brachycladium oblongum (Brn.). Shell-gland complex. Transverse section. *K.G.* Oviduct. *D.G.* Yolk-duct. *Cu.* Cuticle. *D.R.* Yolk-reservoir. *V.D.* Vas deferens. *R.S. Ut.* Receptaculum seminis uterinum. *Oo.* Ootype.

Fig. 7.—Brachycladium oblongum. Longitudinal median section through genital aperture. × 60.

Fig. 8.—Brachycladium oblongum. Longitudinal median section through anterior end, showing pre-pharyngeal pouch. Reconstructed. × 60. *Div.* Pre-pharyngeal pouch.

Fig. 9.—Lebouria idonea n. sp. Ventral view. × 50. *D.R.* Yolk reservoir.

Fig. 10.—Lebouria idonea. Coronal section, anterior end. × 100. *I.D.* Intestinal dilatation.

Fig. 11.—Lebouria idonea. Cirrus-pouch. × 330. *B.Z.* "Begleitzellen."

Fig. 12.—Lebouria idonea. Shell-gland complex. Dorsal view. × 85. *K.G.* Oviduct. *D.G.* Yolk-duct. *D.R.* Yolk-reservoir.

Fig. 13.—Fellodistomum fellis (Olsson). Longitudinal section through dorsal surface and intestinal diverticulum just in front of ventral sucker. × 80. *Cu.* Cuticle with rod-like bodies. *Ep.* Intestinal epithelial cells containing masses of bile (*Z.*).

Fig. 14.—Fellodistomum fellis. Transverse section through centre of ventral sucker. × 75. *C.M.* Circular muscle-fibres of sucker. *D.Z.* Subcutaneous gland cells. *D.Z.S.* Gland cells of the sucker. *G.Z.* "Grosse zellen" (myoblasts?). *I.Z.* Cells of the inner zone. *M.Z.* Cells of the median zone. *P.Z.* Cells of the outer (peripheral) zone.

Fig. 15.—Fellodistomum agnotum n. sp. Ventral view. × 35.

Fig. 16.—Steringophorus cluthensis n. sp. Ventral view. × 55.

Fig. 17.—Plagiorchis notabilis n. sp. Ventral view. × 55. *C.* Cirrus.

Fig. 18.—Spelotrema claviforme (Brandes). Ventral view. × 200. *G.S.* Genital sucker.

Fig. 19.—Spelotrema excellens Mihi. Ventral view. × 130. *G.S.* Genital sucker.

Fig. 20.—Tocotrema jejunum Mihi. Ventral view. × 65. *G.S.* Genital sucker.

Fig. 21.—Tocotrema jejunum. Ventral view. Greatly extended specimen. × 65. *G.S.* Genital sucker.

Fig. 22.—Cryptocotyle concava (Crepl.). Ventral view. × 95. *G.S.* Genital sucker. *D.R.* Yolk reservoir.

Fig. 23.—Cryptocotyle concava. Median longitudinal section. × 240. *G.S.* Genital sucker. *Z.* "Zunge." *Ov.* Ovum.

Fig. 24.—Gymnophallus dapsilis Mihi. Ventral view. × 95.

Fig. 25.—Maritrema gratiosum Mihi. Ventral view. × 110.

Fig. 26.—Maritrema lepidum Mihi. Ventral view. × 100.

Fig. 27.—Maritrema humile Mihi. Ventral view. × 180.

Fig. 28.—Podocotyle atomon var. dispar. Ventral view. × 45. *U.D.* Unpaired group of yolk-follicles. *D.R.* Yolk reservoir. *D.G.* Longitudinal yolk-duct.